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PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON
167th Session (1954-55)

Vol. 167

Part 1

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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

Session 1954-55

Vol. 167

Part 1

PROCEEDINGS OF THE GENERAL MEETING HELD ON 7 October 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the Anniversary Meeting held on 24 May 1954, having been circulated, were taken as read, and confirmed.

The PRESIDENT read a telegram received in reply to the Loyal Message, sent on the day of the Anniversary Meeting, to Her Majesty The Queen, Patron of the Society, upon her safe return from the Commonwealth tour.

The PRESIDENT read a letter from Mrs. Fritsch thanking the Fellows for their Resolution of Sympathy on the death of Professor F. E. Fritsch, F.R.S.

The following were thanked for gifts made to the Library since the last Meeting:—Institut Pasteur, Mr. A. A. Bullock, Mr. Richard Morse, the executors of the late Mr. A. A. Pearson, the French Embassy, the British Society for the History of Science, Mr. F. A. Sowter, Dr. H. S. Holden, the Secretary of the Cactus Society, the National Institute for Medical Research, Prof. N. Polunin, Miss E. M. Stephenson, the Crown Agents for Overseas Governments, Mr. R. E. Dean, Prof. J. Cohen, Prof. James Small, Prof. Otto Jaag, the Forestry Commission, Mr. H. H. Bloomer, Mr. E. Milne-Redhead, Mr. M. R. Qureshi, Dr. R. H. Ahrenfeldt, Mr. A. W. Exell, Dr. F. A. Mendonça, Mr. W. R. Price, Prof. E. P. Stebbing, Dr. J. E. Hamilton, Mr. B. Verdcourt, Miss Annie Hall, Dr. A. J. T. Janse and Mr. D. Wragge Morley.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows:—Mr. Eric John Perkins, B.Sc., Dr. Cecil W. Miles, Mr. Alexis Bogdan, The Rev. Dr. W. Rees-Wright, M.Sc., Mr. Arthur Rhys Beddows, M.Sc., and Dr. Merfyn Richards, M.A., M.Sc.

The PRESIDENT reported the deaths of Professor Herman Augustus Spoehr, F.M.L.S., Professor James Peter Hill, F.R.S., Linnean Medallist, and Dr. Edward Stuart Russell, O.B.E., F.L.S., and moved the following Resolution, which was passed in silence, all present standing in their places:—

The Fellows of The Linnean Society of London, having heard with the very deepest sorrow of the death of Dr. Edward Stuart RUSSELL, O.B.E., F.L.S., desire to place on record their high appreciation of the service rendered to the Society during his thirty years of Fellowship. Elected in 1924 he served on the Council from 1926-30 and 1940-44. He was appointed Vice-President 1943-44 and held the office of President from 1940-43. During his long Fellowship of the Society he showed the greatest interest in all its activities.

Deploring the great loss of so distinguished a Fellow, the Fellows desire to express to Mrs. Russell their deepest sympathy in her bereavement.

The following communications were read and discussed :—

Dr. M. A. Pocock. South African parasitic Florideae and their hosts. 3. Four minute parasitic Florideae. (Discussed by Dr. E. M. Delf and Prof. C. T. Ingold ; Dr. Pocock replied.) **[Printed in full on p. 11.]**

Mr. P. R. Bell. A statistical approach to the problem of the phylogeny of a genus of Ferns. (Discussed by Dr. R. Melville, Mr. E. J. H. Corner, Prof. C. T. Ingold and Dr. E. M. Delf ; Mr. Bell replied.) **[Printed in full on p. 41.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 21 October 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 7 October 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Professor L. J. Audus and Mr. C. E. Hubbard.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Dr. Margaret May Collis and Mr. Humphrey Morrison Burkill, M.A.

The PRESIDENT reported the death of Miss Rosamund Flora Shove, Fellow.

Certificates of recommendation for election to Fellowship were read for the first time in favour of the following :—Kathleen Mabel Archard, B.Sc., John Alan Barker, B.Sc., A.L.S., James Eldred Cuthbert Brokenshire, Alan John Brook, B.Sc., Ph.D., A.L.S., Keith Bissill Carlisle, B.Sc., Professor P. S. Chikkannaiah, M.Sc., Bryan John Culliford, B.Sc., Edward Holt Eason, M.A., M.B., B.Ch., M.R.C.S.(Eng.), L.R.C.P.(Lond.), Harold George Hillier, Miss Joan E. Heriot, M.Sc., K. N. Narayan, M.Sc., Ph.D., Professor Richard Denison Purchon, B.Sc., Ph.D., Miss Ursula K. Smith, B.Sc., John Eustace Sirett Souster, Phillips Arthur Richard Street, M.Sc., Graham S. Thomas, John Griffith Vaughan, M.Sc., Ph.D., A.L.S., and Geoffrey H. S. Wood, M.A.

The following communications were read and discussed :—

Dr. C. B. GOODHART, Genetic stability in populations of the snail *Cepaea nemoralis* (L.) (Discussed by the President, Dr. G. S. Carter and the Zoological Secretary ; Dr. Goodhart replied.) **[Printed in full on p. 50.]**

Mr. F. EVANS. A general account of the Anglo-Belgian oceanographical expedition to the North Equatorial Current of the Atlantic Ocean conducted in the 12 ton yacht 'Petula' and from a towed raft, 1953-4. (Discussed by the President, the Zoological Secretary and Prof. H. Munro Fox ; Mr. Evans replied.)

The following papers were read in title :—

'Spiders from Western Samoa.' By B. J. MARPLES, F.L.S. (Printed in *Journ., Zool.*, No. 287.)

- 'The morphology and growth of the vegetative and reproductive apices of *Arabidopsis thaliana* (L.) Heynh., *Capsella bursa-pastoris* (L.) Medic., and *Anagallis arvensis* L.' By J. G. VAUGHAN, F.L.S. (Printed in *Journ., Bot.*, No. 359.)
- 'The taxonomy and origins of the cultivated bananas.' By N. W. SIMMONDS, F.L.S., and K. SHEPHERD. (Printed in *Journ., Bot.*, No. 359.)
- 'Systematic and ecological notes on the Cladocera of Lake Toba and the surrounding country, North Sumatra.' By D. S. JOHNSON. (Communicated by Dr. J. P. Harding, F.L.S.) (Printed in *Journ., Zool.*, No. 289.)
- 'On some new Acarina, Mesostigmata, from Australia, New Zealand and New Guinea.' By H. WOMERSLEY, A.L.S. (Printed in *Journ., Zool.*, No. 288.)
- 'Journey to Northern Ethiopia (Simien), 1952-53 : Arachnida, Opiliones.' By C. Fr. ROEWER. (Communicated by Dr. Hugh Scott, F.R.S., F.L.S.) (Printed in *Journ., Zool.*, No. 290.)
- 'Journey to the Gughé Highlands (Southern Ethiopia), 1948-49 : Coleoptera, Psephenidae ; the Immature Stages of *Eubrianax scotti* Pic. By C. E. Dyte. Communicated by Dr. Hugh Scott, F.R.S., F.L.S.) (Printed in *Journ., Zool.*, No. 290.)
- 'Journey to Northern Ethiopia (Simien), 1952-53 : Three species of *Phenacolimax* (Gastropoda, Vitrinidae) with notes of the Taxonomy of the Genus.' By LOTHAR FORCART. (Communicated by Dr. Hugh Scott, F.R.S., F.L.S.) (Printed in *Journ., Zool.*, No. 290.)
- 'Insecta Diplura, Japygidae, from Ethiopia.' By Jean PAGÉS. (Communicated by Dr. Hugh Scott, F.R.S., F.L.S.) (Printed in *Journ., Zool.*, No. 290.)

PROCEEDINGS OF THE GENERAL MEETING HELD ON 4 November 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 21 October 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—The President, the Treasurer, Dr. W. G. Templeman, the Institute of Seaweed Research, Inveresk, Mr. A. Bogdon, Dr. H. P. Fuchs, Miss Stella Ross-Craig, Mr. D. K. McE. Kevan, Dr. Johannes Lid., the Freshwater Biological Association, the Zoological Society of London, His Honour Judge Drysdale Woodcock, Q.C., Dr. J. L. Cloudsley-Thompson and Dr. C. R. Metcalfe.

A certificate of recommendation for election to ordinary Associateship was read for the first time in favour of Miss Margaret Pereira, B.Sc., and certificates of recommendation for election to Fellowship were read for the second time in favour of those candidates whose names appear in the Minutes of the Meeting held on 21 October 1954.

The following communications were read and discussed :—

Dr. H. S. HOLDEN. Some features in the morphology of a new pteridosperm stem from the Coal Measures. (Discussed by Dr. Marie Stopes, the Botanical Secretary and Mr. E. J. H. Corner ; Dr. Holden replied.)

Abstract,—

The stem, which has a stellate outline resulting from the decurrent leaf bases, is monostetic with a small pith surrounded by a cylinder of homogenous metaxylem tracheids.

The protoxylem, which is mesarch, forms a number of discrete peripheral groups, each of which is overarched by centrifugally developed metaxylem tracheids. The leaf trace, which is also mesarch, is relatively large and is very similar to that of *Heterangium grievii*. The stem is considered to be that of a pteridosperm related to *Heterangium* and other genera of the Lyginodendreae. (The full account of this paper is printed in *Journ., Bot.*, No. 359.)

THE BROWN TROUT RESEARCH LABORATORY, PITLOCHRY.

Mr. K. A. PYEFINCH. Introductory remarks.

Mr. A. V. HOLDEN. Observations on the addition of chemical nutrients to small lakes.

Dr. A. J. BROOK. The botanical problems of freshwater fisheries research.

Mr. T. A. STUART (paper read by Mr. K. A. Pyefinch in the absence of the author). The selection of spawning grounds by trout.

(In a general discussion of the papers the following took part :—Dr. E. M. Delf, Mr. A. H. G. Alston, Mr. R. Ross, Dr. E. Trewavas, Dr. R. Melville and the Botanical Secretary ; Mr. Pyefinch, Mr. Holden and Dr. Brook replied.) [Abstracts printed on p. 67.]

PROCEEDINGS OF THE GENERAL MEETING HELD ON
18 November 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 4 November 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. F. H. Lancum, M.B.E., Dr. W. M. Docters van Leeuwen and the Society for the Promotion of Nature Reserves.

The PRESIDENT reported the death of Sir John Stanhope Arkwright, Kt., M.A., Fellow.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected. FELLOWS :—Kathleen Mabel Archard, B.Sc., John Alan Barker, B.Sc., A.L.S., James Eldred Cuthbert Brokenshire, Alan John Brook, B.Sc., Ph.D., A.L.S., Keith Bissill Carlisle, B.Sc., Professor P. S. Chikkannaiah, M.Sc., Bryan John Culliford, B.Sc., Edward Holt Easton, M.A., M.B., B.Ch., M.R.C.S.(Eng.), L.R.C.P.(Lond.), Harold George Hillier, Miss Joan E. Heriot, M.Sc., K. N. Narayan, M.Sc., Ph.D., Professor Richard Denison Purchon, B.Sc., Ph.D., Miss Ursula K. Smith, B.Sc., John Eustace Sirett Souster, Phillip Arthur Richard Street, M.Sc., Graham S. Thomas, John Griffith Vaughan, M.Sc., Ph.D., A.L.S. and Geoffrey H. S. Wood, M.A. ORDINARY ASSOCIATE :—Miss Margaret Pereira, B.Sc.

The following communications were read and discussed :—

Mr. R. H. JEFFERS. The Collected Correspondence of Richard Pulteney, M.D., F.R.S. (1730–1801). (Discussed by Dr. J. Ramsbottom and Dr. George Taylor).

Abstract,—

The collected correspondence of Richard Pulteney, M.D., F.R.S., includes some of that of his wife, Mrs. Elizabeth Pulteney (née Galton) (1739–1820) and was presented to the Society in 1953 by Mr. J. H. Robins. It covers the period 1747 to 1801, and has now been chronologically arranged. An account was given of its nature, and of some of the contributors to it. Pulteney was a botanist and conchologist and the first English biographer of Linnaeus, whose system he helped to introduce. He was an apothecary and surgeon in Leicestershire and practised in Dorsetshire as a physician. (To be printed in full in a later part of the *Proceedings*).

Mrs. D. P. WILSON. Mrs. A. W. Griffiths of Torquay and the early history of marine botany in Britain. (Discussed by the President, Miss C. I. Dickinson, Mr. A. H. G. Alston, Dr. J. Ramsbottom and Dr. George Taylor; Mrs. Wilson replied.)

Abstract,—

Amelia Warren Griffiths of Torquay (1768–1858) was an enthusiastic and discriminating collector of British seaweeds who did much to further their study in days when they were little known or noticed. She had a wide acquaintance with contemporary botanists, with whom her reputation stood high, but nothing has been written of her life. An examination of some 110 of her letters and other sources of evidence enabled a brief account of it to be given. Mention was also made of some interesting personalities among the pioneers of marine botany. The talk was illustrated by lantern slides.

PRESIDENT'S RECEPTION

2 December 1954

The PRESIDENT, Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., received the Guests in the Library.

A film of the Anglo-Belgian oceanographical expedition to the North Equatorial Current of the Atlantic Ocean conducted in the 12 ton yacht 'Petula' and from a towed raft, 1953–54, was shown by Mr. F. Evans, with a commentary.

EXHIBITS IN THE LIBRARY.

ROYAL BOTANIC GARDEN, EDINBURGH. Some papers of John Hope, M.D., F.R.S., Regius Keeper of the Royal Botanic Garden, Edinburgh, and Professor of Botany in Edinburgh University, 1761–1786. (Shown by Mr. B. L. Burtt.)

Hope was a staunch advocate of the Linnaean system of classification, but did not necessarily agree with its author on minor points of taxonomy. One item in the exhibit showed specimens and an illustration of *Lonicera marilandica* L. which he sent to Linnaeus. As a result of studying these Linnaeus transferred the plant to the genus *Spigelia*, but he failed to convince Hope, who was strongly of the view that it represented a distinct genus. Hope wrote to Garden, the collector of the specimens, that it was useless to propose a new genus if Linnaeus would not accept it; but he published the plate and article under the name Indian Pink, rather than use *Spigelia marilandica*!

The catalogue of Hope's *Hortus Siccus* shows that he was a keen student of Scottish Botany and he had a number of illustrations made of native plants. Only that of *Ruppia spiralis* is in the Edinburgh papers; the whereabouts of the others, as of Hope's herbarium itself, are at present unknown. Hope sent Linnaeus *Ruppia spiralis* as a new species, but evidently Linnaeus did not accept it and the name was not published till taken up by Dumortier some 60 years later.

Hope published an account of *Eriocaulon* in Skye in 1770: he called it *E. decangulare*. In his catalogue it was originally named *Nasmythia articulata* and that name appears on the proofs of the plate. *Nasmythia* was published by Hudson (*Flora Anglica*, ed. 2, ii, 414-415: 1778), but this evidence suggests that the name was originated by Hope, who also provided reformed generic characters for *Eriocaulon* (Linnaeus, *Mantissa altera*, 167: 1771).

Hope was a correspondent of Stephen Hales and carried out numerous physiological experiments himself. The exhibit showed some of the pictorial records of his experiments. It should be noted that most of these drawings are also represented by black and white copies which were clearly used as lecture diagrams.

REFERENCES.

Eighteenth Century Records of British Plants, in *Notes Roy. Bot. Gard., Edinb.*, 4, 123-190 (1907) [this reprints Hope's catalogue and calendar].
F. Darwin, A Botanical Physiologist of the Eighteenth Century, in *Notes Roy. Bot. Gard., Edinb.*, 4, 241-244 (1909). I. Bayley Balfour in F. W. Oliver, *Makers of British Botany*, pp. 286-290 (1913).

BRITISH MUSEUM (NATURAL HISTORY), DEPARTMENT OF BOTANY.
— Investigations of the Flora of Jamaica, 1687-1954. (Shown by Mr. W. T. Stearn.)

Jamaica, the largest of the British West Indian islands, is 144 miles long, with a maximum width of 40 miles and an area of 4410 square miles; more than half of the island stands above 1000 feet and the Blue Mountains in the east reach 7402 feet at Blue Mountain Peak. Being tropical and having great topographical and climatic diversity, it possesses a rich flora estimated at about 2500 species of flowering plants, 525 pteridophytes and 600 bryophytes. Although about half the size of Wales Jamaica has at least 700 more flowering plants and 180 more pteridophytes than the whole of the British Isles. Probably about 20% of the flora is endemic. When first occupied by the Spaniards, thick forest covered most of the island; very little remains today, the lowlands having been cleared for sugar-cane plantations and the foothills colonized and cultivated by the slaves.

Botanical investigation of Jamaica began with Sir Hans Sloane's visit in December 1687 and his *Voyage to *** Jamaica, with the Natural History* (1707-25), often cited by Linnaeus, provided the foundation of Caribbean botany. Patrick Browne's *Civil and Natural History of Jamaica* (1756) is likewise notable for its wealth of firsthand information on Jamaican plants; his herbarium was purchased by Linnaeus in 1758 for £8 8s. 0d. Between 1859 and 1864 A. H. R. Grisebach published his *Flora of the British West Indian Islands*, based largely on material in the Kew Herbarium. Interest in the flora of Jamaica revived at the end of the 19th century and the need for a new detailed and critical *Flora of Jamaica* became apparent. The preparation of this work was undertaken at the British Museum, (Natural History) in 1908 by William Fawcett with the help of A. B. Rendle. After Fawcett's death in 1926, Rendle continued the work with the help of Spencer Le Marchant Moore. At Rendle's death in 1938 volumes 1, 3-5 and 7 had been published. Between 1938 and 1952 work on the *Flora* was suspended but has now been resumed.

The exhibit illustrated with maps, portraits, books, specimens, drawings and photographs of vegetation the history of the botanical investigation of Jamaica from Sloane's time to the present day.

IMPERIAL COLLEGE OF SCIENCE, FIELD STATION, SUNNINGHILL. An aktograph which records the time, rate and duration, of walking-movements and oviposition, of moths. (Shown by Mr. P. Makings.)

This apparatus records the time, rate, duration and total of walking-movements and, simultaneously, the time, rate, duration and total of oviposition. The working-principles depend upon the moth being suspended so that it rests or walks in a normal position on a light wheel with the tip of the abdomen above, or resting on, the edge of a horizontal circular plate. When the moth walks, the light wheel is turned in 'Treadmill' fashion. This movement is imparted by a spiral collar, on one side of the wheel, to a lever which operates a recording pen. This makes a vertical line on a chart, a horizontal line being produced in the absence of walking-movements. The Chart revolves once in 24 hours and thus records (as vertical lines) the walking-of the moth and the time of occurrence. An electrical contact on the pen-arm activates a counter, which thus records the number of revolutions of the 'Treadmill' and hence the distance walked by the moth. The circular plate, at the top of the apparatus, is mounted on the same drum as the chart and thus revolves, also, once in 24 hours. A large filter-paper on this plate provides a convenient surface on which the eggs are deposited and cemented down by the moth, thus forming an automatic record of the time of deposition. It should be mentioned that these times are worked out by marking the time at the start and finish of an experiment and measuring off hourly intervals. The rates of activity may be worked out by dividing the number of eggs, or revolutions of the wheel, into the time between first and last points of the selected range.

Mr. J. A. BULLOCK. A polymorphic population of Lycid beetles.

ROYAL BOTANIC GARDENS, KEW. The *Index Kewensis* and its Supplements. The new method of incorporating the supplements in one volume now adopted at Kew. (Shown by Mr. A. A. Bullock.)

Mr. R. A. GRAHAM. Re-discovery after 20 years of *Epipogium aphyllum* Sw. 1953.

ROYAL BOTANIC GARDENS, KEW. Studies in *Bromus carinatus*. Drawings and specimens to illustrate the life history, structures and behaviour of an American grass now established in certain parts of England. (Shown by Mr. J. K. O'Byrne.)

KING'S COLLEGE, LONDON, DEPARTMENT OF ZOOLOGY. *Scoloplos armiger*: an example of non-pelagic development in Polychaete Annelids. (Shown by Mr. D. T. Anderson.)

Thorson (1946: Medd. Komm. Danmarks. Fisk., Ser. Plankton B.4) points out that in spite of the fact that polychaete larvae form a very important constituent of marine plankton, it seems very likely that about 75 per cent of polychaetes have a non-pelagic development. In many cases it has not been found possible to make observations to support this idea, owing to the difficulty of obtaining material; but such factors as the absence of larvae from the plankton, Arctic distribution, etc., provide reasonable circumstantial evidence of a mode of development without a free-swimming pelagic stage.

The interest of *Scoloplos armiger* lies in the fact that it provides a perfect example of non-pelagic development in polychaetes and at the same time is a widely distributed littoral form for which developmental material is very easy

to collect. The species occurs in muddy sand and breeds in the early spring (February at Whitstable, later in more northern waters). The main spawning takes place in association with a spring tide (i.e. it has a lunar periodicity) and apparently with a rise in temperature. The eggs are laid in gelatinous cocoons each containing between 800 and 1200 ova, the cocoons being 2 cm. long by 1 cm. broad and being attached to the sand by a stalk some 5 cm. in length.

The eggs are 250μ in diameter and contain a considerable quantity of yolk. After three days development has proceeded as far as a stage which can be regarded as a suppressed trochophore, resembling in many ways the free-swimming trochophore of Serpulids, etc., and having a ciliated prototoch although it is embedded in jelly.

Subsequent elongation and segmentation of the body leads to hatching from the jelly capsule after 10 days. The young worm has by now a functional gut and a co-ordinated muscular system, and immediately burrows in the sand. It feeds on diatoms and other organic matter adhering to the sand grains, ingesting the food by means of a ciliated eversible proboscis. Growth proceeds by the addition of further body segments posteriorly, together with increase in size and complexity of the body as a whole. The adult condition is probably attained after two years.

MINISTRY OF AGRICULTURE, INFESTATION CONTROL DIVISION. *Ephestia elutella* as a pest of stored products in Great Britain. (Shown by Mr. G. A. Brett and Miss E. M. Debenham.)

The exhibit showed, with the aid of maps, something of the World Distribution of *Ephestia elutella* Hbn. (Lep. Phycitidae) and of its occurrence as established infestations in the United Kingdom.

Ephestia elutella is endemic in many warehouses in the main ports of this country, infesting a wide range of commodities, such as wheat, wheat offals and meals, cocoa beans, oilseeds and their products, dried fruit and tobacco. Two methods of spread of infestation within and from the port were indicated in the exhibit by means of photographs of moths in flight in summer and migrating larvae, late summer to autumn. In addition, it was shown that the dispersal of *Ephestia elutella* in infested goods and containers from the ports to inland warehouses, factories, mills, wholesale merchants and retailers continues at all times of the year. Distinguishing characters of the adults of *E. elutella* and of *E. cautella* were demonstrated in mounted specimens and preparations of the dissected genitalia for examination under the binocular microscope. Characters used in separating the larvae of the two species were also displayed.

The specimens of damaged commodities resulting from infestation by *Ephestia elutella* emphasized the serious nature of the problem in this country.

MINISTRY OF AGRICULTURE, INFESTATION CONTROL DIVISION. Warfarin as a Rodenticide. (Shown by Miss M. D. A. Lawrence and Mr. R. A. Davis.)

The most recent development in rodenticides is the use of blood anticoagulants. They have the advantage of being cumulative poisons which, when ingested regularly, in small doses, cause fatal haemorrhages. In rat and mouse control operations they are used over a period of several days at a low concentration in baits; ingestion of the small doses building up to the lethal dose or more, does not apparently produce unpleasant symptoms which are associated with the food supply. At the concentrations advised, namely 0.005 or 0.025 per cent by weight in a cereal base, rats continue to feed upon the bait until death. It is therefore unnecessary to condition rats to feed freely upon unpoisoned bait before adding the poison.

The exhibit showed slides, photographs and dissections of normal rats (*Rattus norvegicus* Berkenhout), compared with those killed with the anti-coagulant Warfarin [3-(α -phenyl-betaacetyethyl)-4 hydroxycoumarin]. Warfarin prevents the formation of thrombin by interfering in some way with the prothrombin, thromboplastin reaction and normal clotting of the blood does not occur. It is also thought to initiate some damage to the capillary walls. These two effects together with normal wear and tear on tissues result in spontaneous haemorrhages which cause the death of the animal.

MINISTRY OF AGRICULTURE, INFESTATION CONTROL DIVISION. Myxomatosis. (Shown by Mr. H. V. Thompson, Major C. J. Armour and Mr. M. G. Ridpath.)

ROYAL BOTANIC GARDENS, KEW. Two specimens of Grass (*Triplopogon ramosissimus* (Hack.) (Bor), 12-15 feet tall, endemic in Bombay State. (Shown by Dr. N. L. Bor.)

This annual grass (a member of the *Andropogoneae*) is endemic in Bombay State, India, where it grows in large clumps on stony hillsides or near the seashore on slopes that have been cleared of forest.

It is remarkable for the way in which the stem is supported above the surface of the soil by numerous stilt roots.

The seeds germinate in the ordinary way, but shortly after germination stilt-roots are developed from the lowest node above ground, and they and those subsequently developed from nodes above take over the supply of nutrient from the soil. The base of the plant and the original roots disappear leaving the culms supported above the soil much in the same way as the stem of a mangrove.

A further point of interest is the leaf-blade. This is reduced in the lower portion of the blade to the midrib, so that the leaf becomes distinctly petioled—an uncommon feature in the *Gramineae*. (Grown in one of the Tropical Houses at Kew.)

LONDON SCHOOL OF HYGIENE AND TROPICAL MEDICINE, DEPARTMENT OF PARASITOLOGY. Tissue stages of Malaria and Malaria-like parasites in various Mammals. (Shown by Professor P. C. C. Garnham.)

Less than ten years ago the tissue cycle of mammalian malaria was unknown, though its existence had been suspected from the beginning of the century. First in bats, then in monkeys and later in man, the tissue stages were discovered, and today, the details of this part of the life cycle of many mammalian parasites are clear. The following examples were shown in the demonstration :

PRIMATES :

Man	<i>Plasmodium vivax</i>	
	<i>Plasmodium falciparum</i>	
	<i>Plasmodium ovale</i>	
Oriental Monkeys	<i>Plasmodium cynomolgi</i>	
	<i>Plasmodium inui</i>	
	<i>Plasmodium knowlesi</i>	
African Monkeys	<i>Hepatocystis kochi</i>	
Madagascar Lemur	<i>Plasmodium foley</i>	[Unknown]

EDENTATES :

Fruit Bats	<i>Hepatocystis epomophori</i>	
	<i>Hepatocystis pteropi</i>	[Unknown]
Insectivorous Bats	<i>Polychromophilus murinus</i>	
	<i>Nycteria medusiformis</i>	
Elephant Shrews	" <i>Plasmodium</i> " <i>brodeni</i>	[Unknown]

RODENTS :

Flying Squirrels	<i>Hepatocystis vassali</i>	
Congo Rats	<i>Plasmodium berghei</i>	[Unknown]

ANTELOPES :

Sitatunga	" <i>Plasmodium</i> " <i>limnotragi</i>	[Unknown]
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With the single exception of *P. murinum* of insectivorous bats, the cycle of every parasite takes place in the parenchyma cells of the liver, where the species closely resemble one another in general morphology. There are differences in detail, however, on which an identification can be made.

Malaria parasites are particularly found in the Primates and in Bats, and are transmitted by mosquitoes and other biting insects. The reason for their absence in the other orders is unknown.

QUEEN MARY COLLEGE, LONDON. A series of photographs and diagrams illustrating morphological distinctions between the three species of the Genus *Durvillea* in New Zealand. (Shown by Miss Margaret Naylor.)

The genus *Durvillea* Bory 1826 is represented in New Zealand by three species, *D. antarctica* (Chamisso) Hariot 1892, *D. willana* Lindauer 1949 and *D. caepestipes* (Mont.) Skotts. 1907. The photographs and diagrams illustrated the main morphological distinctions between the three species and a few points of taxonomic interest were discussed and illustrated.

ROYAL BOTANIC GARDENS, KEW. Illustrations for the *Flora of West Tropical Africa*, new edition. Examples were shown of the plates prepared recently of West African plants. (Shown by Mr. F. N. Hepper and Mr. R. W. J. Keay.)

THE ZOOLOGICAL SOCIETY OF LONDON. A small collection of Birds, Reptiles and Crabs including Frogmouth, Guira Cuckoo, Brazilian Hangnest, Puff Adder and young, Common Viper and young, and a Robber Crab. (Shown by Mr. L. C. Bushby and Mr. J. Yealland.)

PROCEEDINGS OF THE GENERAL MEETING HELD ON 20 January 1955

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 18 November 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. Agnes Arber, F.R.S., Dr. N. L. Bor, C.I.E., Dr. F. Børgesen, Mr. M. R. Henderson, Professor J. W. Heslop Harrison, F.R.S., Mr. Richard Morse, Dr. G. W. Reynolds, Dr. H. Santapau, S.J., Col. F. C. Stern, O.B.E., M.C., Dr. R. E. Vaughan, Miss E. M. Wakefield, O.B.E., Miss Edith M. Wood, the John Innes Horticultural Institution and Messrs. Allen & Hanbury, Ltd.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. John Eustacé Sirett Souster, Mr. Peter Humphry Greenwood, B.Sc., Mr. John Alan Barker, B.Sc., Dr. Edward Holt Eason, M.A., Dr. John Griffith Vaughan and Mr. Bryan John Culliford, B.Sc.

The PRESIDENT reported the following deaths :—Professor Richard Eric Defoe Baker and Henry Atkinson, Fellows.

The following communications were read and discussed:—

Miss D. J. JACKSON. The Capacity for flight of Water Beetles, with observations on various species occurring in the Western Scottish Isles. (Discussed by Dr. Julian S. Huxley, Dr. G. S. Carter, Mr. G. J. Kerrich, Mr. E. Milne-Redhead, Asst. Prof. H. R. Hewer and Dr. George Taylor; Miss Jackson replied.) Contributions to the Discussion from Prof. F. Balfour-Browne and Prof. J. W. Heslop Harrison were also read. [Printed in full on p. 76.]

Dr. W. A. CLARK. Plant Distribution in the Western Isles. (Discussed by Mr. E. J. H. Corner, Mr. P. J. Wanstall, Mr. G. J. Kerrich, Dr. H. Hamshaw Thomas, Dr. R. T. Porsild, Dr. A. Tindell Hopwood, Mr. P. R. Bell, Mr. R. W. J. Keay, Asst. Prof. H. R. Hewer and Dr. George Taylor; Dr. Clark replied.) [Printed in full on p. 96.]

Professor J. W. HESLOP HARRISON, F.R.S., on field studies of the distribution of the plants and animals of the Scottish Western Isles. [Abstract printed on p. 103.]

SOUTH AFRICAN PARASITIC FLORIDEAE AND THEIR HOSTS

3. FOUR MINUTE PARASITIC FLORIDEAE

By M. A. POCKOCK*.

(With 6 Plates and 6 text-figures.)

SYNOPSIS.

Four small parasitic Florideae are recorded and observations on their structure, development, reproduction and occurrence described.

The cosmopolitan *Choreonema thureti* is recorded for the first time from South Africa, where it is widespread and of comparatively common occurrence.

Episporium centroceratis, previously known only from West Australia, is recorded from several stations. The description given by Möbius is shown to be based on an erroneous interpretation; an emended diagnosis is given and further details of structure and development added. Possible affinities are considered.

Two new genera each with a single species are described:—*Aiolocolax pulchella*, parasitic on *Falkenbergiella caespitosa*, is widespread on both the west and east coasts. *Onychocolax polysiphoniae*, parasitic on *Polysiphonia incompta*, is apparently confined to the warmer waters of the east coast. In both, details of structure and reproduction are described and possible affinities considered.

The systematic positions of the three latter are discussed. *Onychocolax* is tentatively assigned to the Lophothaliaceae among the Rhodomelaceae. The positions of *Episporium* and *Aiolocolax* are still doubtful; the former shows some affinity with the Choreocolacaceae generally included in the Cryptonemiales, but differs in some important characters. *Aiolocolax* most nearly approaches the Ceramiales but cannot be placed in any of the families at present recognized.

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INTRODUCTION.

The comparatively insignificant number of very diverse Red Algae which, by virtue of their habit alone, may be classed together as Parasitic Florideae includes forms which are all small—the largest, *Pleurostichidium*, may reach

* Part of this work was done during the tenure of Senior Bursaries granted by the C.S.I.R. of S. Africa for work on algae.

a length of 2 cm., the others are seldom more than a few millimetres in size—but which are nevertheless usually fairly easily discernible by the naked eye, particularly when freshly gathered, since the living parasite, hyaline and completely colourless, stands out in sharp contrast against the strongly pigmented host.

During the past decade thirteen parasitic red algae have been collected on South African coasts; most of these have already been recorded in the preceding paper of this series (Martin & Pocock, 1953) but in addition four microscopic species were found, which form the subject of the present paper. Possibly yet others remain to be discovered.

Of the four, one, *Choreonema*, though here recorded for the first time from South Africa, is world wide in its distribution; two, *Aiolocolax* and *Onychocolax*, are entirely new both as regards species and genus: finally, the fourth and largest, *Episporium*, the hemispherical pustules of which may reach a diameter of as much as half a millimetre, is perhaps the most interesting of the four, since the only previous record, based on a single collecting, is from West Australia.

Since the four genera are very different from one another and obviously not closely related, treatment in each case varies somewhat. *Choreonema* presents no special taxonomic problem, hence the records of its occurrence and geographical distribution need only be supplemented by brief observations. In *Episporium* the historical aspect is naturally stressed and an emended diagnosis becomes necessary. The systematic position of each of the three genera, *Episporium*, *Aiolocolax* and *Onychocolax*, presents a different problem; it has therefore seemed best to discuss each separately, while a general discussion is given at the end of the paper.

Methods. Wherever possible examination of fresh material has been made. Various fixatives have been used. Formalin acetic alcohol proved to have certain disadvantages; acetic alcohol gave rather better results, but on the whole fixation in Neutral Formalin ($2\frac{1}{2}$ per cent Formaldehyde in sea water, neutralized with Hexamethylenetetramium) was the best. Whole mounts and squashes have been used throughout, stained in various ways. Aniline Blue differentiated with Hydrochloric acid was only moderately successful: Harris's Haematoxylin gave good results in some cases, but on the whole the most satisfactory method proved to be preliminary staining with Aceto-carmine, followed after removal of excess carmine with 45 per cent acetic acid by a dilute solution of fast green in glycerine, run in under the cover slip and drawn through repeatedly with filter paper. Excess green is removed by running in 60 per cent and finally pure glycerine, after which the preparation may be sealed with varnish. Nuclei and pit connections stain up particularly well and remain clearly demarcated, but probably owing to acidity of the medium, the fast green fades after a few days to a bluish or purplish tint. Use of the oil immersion lens is essential. Even when initial fixation is unaccompanied by shrinkage, during the process of staining there is often considerable shrinkage of the protoplast accompanied by an expansion of the outer membrane. This shows in some of the photographs, particularly in the case of *Aiolocolax*.

I. CHOREONEMA Schmitz, 1889.

Choreonema thureti (Born.) Schmitz. (Pl. I, figs. A, B.)

Dimensions.

Conceptacles	90–100 μ wide by	80–100 μ high
„	140–160 μ „	„ 120–160 μ „
„	120–140 μ „	„ 100–120 μ „

Occurrence. Parasitic on *Jania**. Conceptacles often in very great numbers on a single branch of the host.

Geographical Distribution. Cosmopolitan; in S. Africa widespread but sporadic. *Jania* from many localities has been examined without any sign of the parasite being found, but when present, often in great abundance, and to be expected wherever the host occurs.

Richest occurrence yet observed: Muizenberg, May 1951 (9297, etc.). Also found at Strandfontein, east of Muizenberg (9302).

In the Eastern Province probably common; collected at the Kowie (Salt Vlei, 9303); Cove Rock (9155); Morgan Bay (9302).

Natal: Chaka's Rock (9610); Isipingo (9933).

Observations. The South African material appears to be identical with the European *Choreonema thurcti* except that the conceptacles tend to be slightly larger and the ostiole rather more protuberant.

Suneson (1937) has recently re-investigated this interesting little coralline parasite; his figure (25 A) shows well the filamentous plant body within the host tissue from which the external fructifications arise.†

II. EPISPORIUM Möbius, 1885.

Episporium centroceratis Möbius (1885). (Figs. 1 and 2; Pl. 1. figs. C–J.)

Dimensions.

Mature branches:

♂ $-316\ \mu \times -212\ \mu$

♀ $269-474\ \mu \times 269-395\ \mu$; cystocarps 6–14; 79–95 μ in diameter

⊕ $252-490\ \mu \times 174-341\ \mu$; central cell $47-84\ \mu \times 140-146\ \mu$

Occurrence. Parasitic on *Centroceras clavulatum*, but hitherto found only on low stunted plants growing in dense tufts in gullies washed by waves even at low tide, or on rocks near the edge of the reefs fringing a bay. Sporadic in its incidence, but when found on a single tuft of the host usually present in fair numbers, most often on the younger erect branches; sometimes crowded at the young actively growing apices (Pl. I, E).

Geographical Distribution. Recorded from Dirk Hartog Island, West Australia (Type locality).

In South Africa hitherto found only at six stations on the east coast but probably more widely distributed than appears.

Eastern Province: The Kowie (a) gully near Salt Vlei, 9 November 1946 and again 24 November (9304), and (b) Shark's Bay, on rocks at east side of bay 2 September 1951 (9350); Cove Rock, west of East London, 20 February 1948 (9140); Kasouga, the Ship Rock, January 1951 (9305). Port Elizabeth, Lighthouse Beach 26 May 1956 (11372).

Natal: Isipingo, 28 October 1951 (10192).

The curious little alga to which Möbius gave the name of *Episporium* derived from material of *Centroceras* handed to him by Askenasy who was working on the algae collected by Dr. Naumann on the voyage of the frigate "Gazelle". This original record, from Dirk Hartog Island off West Australia, almost within the Tropics (latitude 26° S.), has apparently remained unique. But the host, *Centroceras clavulatum*, is widespread, particularly in southern waters. On the coasts of South Africa it is one of the commonest of the medium-sized Rhodophyceae, often covering wide areas of rock as a close turf, or forming large tufts a couple of inches or more in height, in pools, gullies, etc. It seemed reasonable therefore to suspect that the parasite too might occur there, and search was made repeatedly; but quantities of *Centroceras* from numerous localities both at the Cape and in the Eastern Province were examined in vain. Finally, mixed with a clump of *Polysiphonia incompta*

* Since the above was written, *Choreonema* has been found on other species of *Jania* and also on *Cheilosporum cultratum* (St. James, 11245) where it causes marked hypertrophy.

† Dr. Suneson has very kindly examined some of the S. African material and has confirmed my diagnosis of the species; apart from the slightly larger size he finds no appreciable difference.

In line 24 on this page the sign ⊕ represents a tetrasporangian.

(collected for the sake of another parasite, *Onychocolax*), stunted plants of *Centroceras* were found and on them, here and there, were small, more or less hemispherical excrescences which proved to be tetrasporic pustules of the missing parasite. The plants were growing in a narrow wave-scoured gully beyond Salt Vlei and fortunately the actual spot in the extensive reefs could be identified with some degree of accuracy; the following spring tide it was revisited and further material, still rare but much more complete than the first collecting, was obtained. This included a range of male, female and tetrasporic pustules in all stages of development and made it possible to obtain a very good idea of the alga in many different stages. Unfortunately, however, it was not possible to study this material in detail immediately after collecting and consequently certain observations, particularly as to colour, proved misleading. Two years later, however, *Episporium* was found again, this time at Cove Rock, and examination of freshly gathered material made it possible to correct the earlier observations. Since that time it has been collected at three other stations*—the Ship Rock, Kasouga (mostly very young pustules), Shark's Bay also at the Kowie but some distance from the original locality, and at Isipingo in Natal. It is probably widespread in the warmer regions of South Africa, but even when relatively abundant is so small—even fully grown pustules are under half a millimetre in diameter—that collecting it involves microscopic examination of the host, branch by branch, and even then it is easily overlooked. Hitherto it has been found only on short, stunted and probably rather old plants of *Centroceras*, never on the young vigorous plants, some two or more inches tall, which more commonly come under observation. Moreover, it is markedly sporadic; in material collected from a single small area, one part of a clump of the host may bear *Episporium* in quantity, while the rest of it and many neighbouring clumps show no sign of the parasite.

The South African plant is identical with that from West Australia, both as regards genus and species; comparison with the careful description (allowing for the error in interpretation) and drawings given by Möbius (1885, p. 77 et seq.), all the more admirable when one considers that he was working with material fixed some time previously in alcohol, puts its identity beyond doubt and it is therefore possible to amplify the description given by him and to correct the basic error in interpretation which led to the, in the circumstances, unhappy choice of a generic name.

Möbius chose the name *Episporium* in the belief that the little plant was 'epiphytic' on tetrasporangia of *Centroceras*. It was unfortunate that, apparently, only tetrasporic plants of the *Centroceras* in the original collection were infected; actually, apart from the usual similarity of position, *Episporium* has nothing whatsoever to do with the tetrasporangia of *Centroceras* and, so far as at present known, is never parasitic on them. The structure which Möbius (l.c., p. 78) took to be the undivided contents of an abnormal tetrasporangium is the central and first-formed cell of the parasite itself. In the earlier South African material the infected plants were rarely fertile, but when parasite and tetrasporangia do occur on the same branch the difference between the two is evident (fig. 1, j; Pl. 1, E). A very misleading phenomenon is the deep pigmentation of this central cell in material which has been kept for some time before examination or fixation. In a preliminary account of the parasite read before the Royal Society of South Africa in 1947 this apparent 'pigmentation' was commented on as being unusual in parasitic Florideae. Subsequently, however, it was found that when fresh, the whole parasite, central cell included, is entirely devoid of pigment of any kind, no chromoplasts being formed in any of the cells; it is only as degeneration begins that coloured cell sap leaches out from the host cells, concentrating in the central cell of the parasite until it is as deeply coloured as the tetrasporangia of its host.

*Recently collected also at Port Elizabeth (Lighthouse Beach)

Another very striking feature is the stout, conspicuous protoplasmic processes connecting the central cell with the radiating rows of small cells which build up the tissue of the pustule (Pl. 1, H). Since Möbius expressly refers to the absence of protoplasmic connections, they had probably been lost in fixation. Possibly these two facts alone sufficed to mislead Möbius in his interpretation of the nature of the organism with which he was dealing. It is obvious that an emended diagnosis of the genus *Episporium* is necessary. The following description is based on that given by Schmitz (1897, p. 502), modified and amplified by the study of the South African material:—

Episporium Möbius. Emended diagnosis.

Parasitic: mature thallus a small cushion consisting of many repeatedly branching rows of cells radiating from the upper end of a large central cell the base of which is attached to the host and which continues growth as the cushion develops.

Reproductive organs formed in the outer layers of the cushion. Tetrasporangia cruciately divided. Carpogonial branch three-celled, borne laterally near the apex of the bearing cell. Cystocarps many, without cellular investment but enclosed in a protuberance of the common membrane.

Only species: *Episporium centroceratis* Möbius.

Mature plant more or less hemispherical reaching almost half a millimetre in diameter, with the broad base closely adpressed to the surface of the host, completely surrounding the central cell. Lower end of central cell penetrating between the cortical cells of the host to make contact with the central cell; at first simple, later more or less lobed, each lobe forming a haustorial organ attached to the host cell; upper end much swollen with thick protoplasmic projections connecting it with the rows of small cells forming the cushion, so that it has the appearance of a mace head.

Erect axes most often solitary, sometimes several at a node; occasionally in small groups from a single internodal infection, rarely branched. In the asexual pustule tetrasporangia very numerous formed over the whole outer surface of the cushion.

Sexual pustules either dioecious or monoecious; in the male pustule spermatangia covering the whole outer surface, in bisexual pustules in patches between groups of female organs. Carpogonium at first flask shaped with neck projecting into a raised protuberance of the membrane through which the developing trichogyne emerges; mature trichogyne exceedingly long and delicate.

Cystocarps many, more or less hemispherical, scattered over the surface and projecting from it, protected only by a protuberance of the common membrane which enlarges as the cystocarp develops.

Observations. Apparently the spores of *Episporium* most readily find lodgement on the delicate tissue in the angle just above the nodal ring of processes, i.e. in the same position as that in which the *Centroceras* tetrasporangia develop (fig. 1, b, e; Pl. 1, C–F), but not infrequently they may obtain foothold on an internode, particularly in young actively growing branches. As the spore germinates it elongates, the lower end develops into a short rhizoidal process or lobe which penetrates between the cortical cells and makes contact with the central cell of the host, while the upper end continues to elongate and broaden, the whole becoming enclosed in a conspicuous hyaline sheath within which further development takes place. At this stage there is some superficial resemblance to a rather abnormal young *Centroceras* sporangium but both wall and protoplast show obvious differences. The protoplast is granular, dense, multinucleate and without chromoplasts (fig. 1, a–c).

There is great variation in the degree of preliminary enlargement—some germlings are large with wide sheath before any division takes place, whereas

in other cases plantlets barely half the size show cell division already well advanced (compare fig. 1, a & e with fig. 1, b & f of corresponding stages drawn to the same scale). The possibility of size distinguishing young asexual

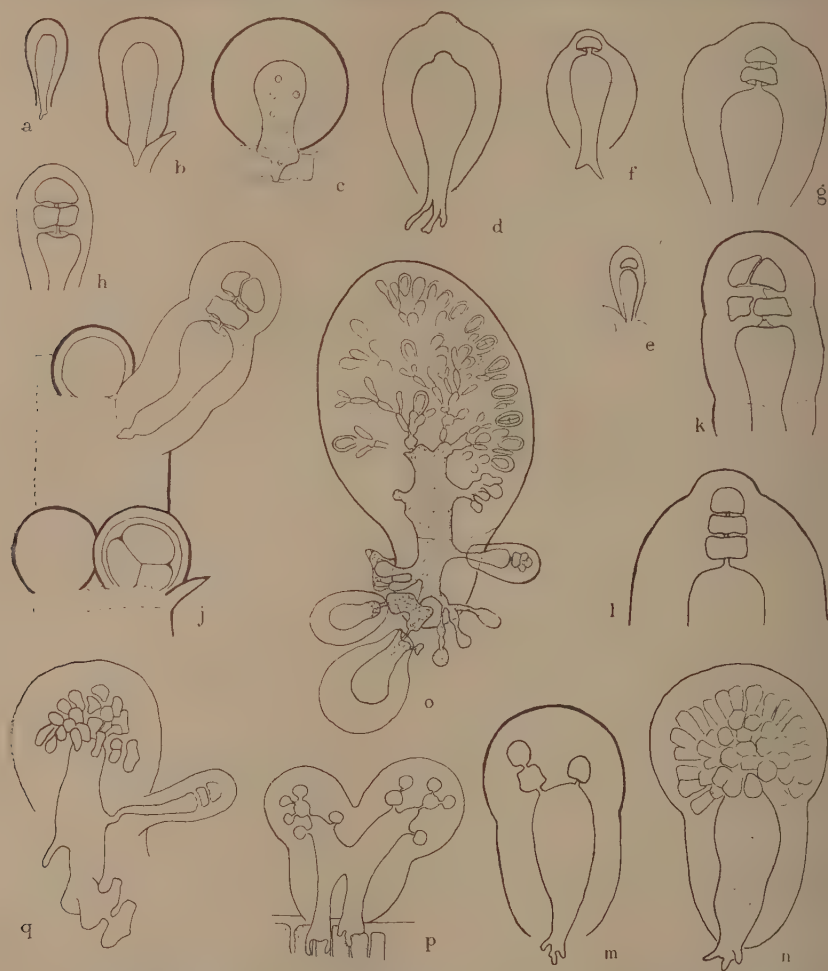


FIG. 1.—*Episporium centroceratis*. Development of the pustule. a–c, developing sporeling, still single celled; in c, penetration of cortical cells of host by basal rhizoidal processes and numerous nuclei shown; d, preparing to cut off first apical cell, attachment organ branching; e, f, first apical cell cut off; g, second cell cut off; h–k, first division in primary cells, in h, lower cell divided, in j, upper cell; in k (older) both cells. Relation to tetrasporangia of host, position of internodal pustule and the primary and secondary sheaths of the developing pustule are shown in j; l, three primary cells cut off before any divide; m, two apical cells cut off adjacent to one another; n, formation of cushion well advanced, attachment organ and nuclei in central cell shown; o, unusually luxuriant internodal tetrasporic pustule, basal portion branching freely, each branch initiating a subsidiary pustule; in the cushion, a few cells indicated to show relation of cell-rows to one another and to the central cell and position of tetrasporangia in the cushion; p, central cell branched, two cushions developing; q, small lateral branch arising from central cell and beginning to form a cushion. o, $\times 200$, all other figures $\times 500$

from sexual plants has been considered but as yet no evidence has been found to indicate that size is in any way related to genetical constitution; it seems to be merely an idiosyncrasy of individual spores.

Eventually division begins: at its upper end the initial cell puts out a small protuberance (fig. 1, d) and an apical cell is cut off transversely (fig. 1, f). In general this divides again transversely once, sometimes twice (fig. 1, g & l) and the resultant cells immediately begin to cut off laterals which initiate repeatedly branching rows of cells. At first sight branching appears to be dichotomous, but actually each cell gives rise to three or more branch-initials; there is soon no trace of the single apical cell. The first branch-system thus initiated is soon followed by others each arising from a cell cut off from the surface of the broadening end of the central cell and remaining connected with it so that the protoplast is drawn out until it has the appearance of an armoured mace-head (Pl. 1, H, J). As development proceeds the constituent cells become progressively smaller, the older cells of the rows become drawn out radially and widely separated laterally, while the younger apical cells are closely aggregated, forming a compact surface layer into which the developing reproductive organs are interpolated. This surface layer is constantly being pushed outwards by continued apical growth and becomes closely adpressed to the enveloping membrane.

The first sheath is soon inadequate and has to be enlarged to keep pace with the growing pustule. In some cases the initial sheath is ruptured and the developing thallus, enclosed in a secondary sheath, emerges (Pl. 1, C, D); in others the secondary sheath originates as a protuberance of the first, enlarging gradually with the growth of the thallus. Sometimes three or more such enlargements may be traced before the final sheath of the pustule is differentiated (fig. 1, k). In the mature pustule the sheath is a tough, transparent, hyaline membrane closely adpressed to the underlying cell-layer and in part at least fused with the cell walls.

Meanwhile, as the size of the pustule increases, further lobing takes place at the lower end of the central cell, each lobe making connection with the host cell and functioning as a haustorial organ (fig. 1, n, m). Most often a single erect axis results from each infection the plant remaining unbranched (Pl. 1, F-H), but in vigorous growths branching of various types may occur. In the most usual type, once development of the initial axis is well advanced, cells are cut off from the base of the central cell and each of these in turn may give rise to an erect axis. When the primary infection is nodal such basal cells may form a filament girdling the node and giving rise to secondary axes; thus several pustules of differing ages, connected with one another, may occur at one and the same node; if, however, it is internodal branching may take place in all directions so that a small clump of axes develops (fig. 1, o). Such cases are, however, rare. In another type of branching an erect axis itself branches; either the central cell becomes lobed at its apex and each lobe proceeds to develop a cushion (fig. 1, p), or more rarely a cell may be cut off laterally and function as the central cell of a secondary pustule (fig. 1, q). Apparently such branching usually becomes obscured during development, since mature pustules are normally remarkably regular in outline.

Development of reproductive organs is progressive, beginning at a very early stage—a male pustule 36μ wide by 72μ high had already formed four spermatangial mother cells, from one of which abstriction of spermatia had begun. On a female axis 47μ wide by 58μ high, six or eight carpogonial branches could be counted, most of them immature but one with the trichogyne already elongating. The smallest asexual pustule measured in which division of the tetrasporangia had begun was 95μ wide and long, while in another slightly larger (126μ by 111μ) the whole surface was already producing tetrasporangia.

The mature tetrasporic plant (Pl. 1, G) is very characteristic, typically regular in outline with slightly sunk, cruciately divided tetrasporangia in various stages of development spread over the whole hemispherical outer surface. When mature the outer end of the sporangium wall fuses with the enveloping membrane of the pustule, a pore is formed and the spores are liberated. The partially collapsed wall of the empty sporangium, held in place by the apical union with the membrane, persists as a columnar structure between the still developing younger sporangia (fig. 2, a). The sporangia are relatively large; when mature, wall $14-18\mu$ by $22-26\mu$, protoplast $9-11\mu$ by $16-21\mu$ (fig. 2, b).

In sexual pustules the position of the reproductive organs is marked by vaulted protuberances of the hyaline envelope, like miniature candle extinguishers, pushed up by the developing spermatangium mother cells, and, slightly larger, by the necks of young carpogonia (fig. 2, c, h). Some pustules are entirely male, and when mature spermatangial cells in all stages of development completely cover the whole of the hemispherical outer surface. The spermatangium mother cells are cut off from outer cells of the cell rows of the cushion, enlarge slightly and from the apex of each first one, then a second and sometimes a third primary spermatangium is cut off obliquely, a protuberance forming above each (fig. 2, c, d); as maturity is reached the spermatium escapes through a pore in the apex of the protuberance. The primary series of spermatangia is followed by one or more secondary series. The two or three protuberances belonging to a mother cell are displaced by mutual pressure so that they project at angles slightly inclined to one another. Since the outer membrane acquires a most characteristic appearance as abscission and liberation of spermatia progresses, a male pustule is readily distinguished from an asexual one, which it much resembles in regularity of shape. In the photograph (Pl. 1, H) the whole of the tissue of the cushion has slipped off the central cell, the 'mace-head' of which can be clearly seen.

In addition to such purely male pustules, however, most of the apparently female pustules examined have proved to be bisexual, more or less extensive spermatangial regions occurring among the carpogonial branches. Such bisexual pustules, which show a strong tendency to protandry, were first noticed in the Shark's Bay material, where they predominated. This led to a re-examination of material from other localities and in these too, with the exception of the Isipingo material (rather scanty), the same phenomenon was found to be present, though at times less general. Usually male and female organs are in separate patches, not intermingled with one another. Even in pustules with maturing cystocarps such male zones can often be distinguished (fig. 2, e & f).

The female pustule is the most distinctive of all. When young, numerous trichogynes, varying in length from short and stumpy, still within the protuberance of the membrane, to very long, slender, thread-like structures, often over 200μ when fully developed, project in all directions (fig. 2, e); in the young plant shown in this figure over 40, the longest 240μ in length, were counted, in addition to many young carpogonial branches. Eventually the much enlarged pustule becomes very irregular in outline, the numerous more or less hemispherical cystocarps in varying stages of development projecting from the surface, protected only by a bulging layer of the common envelope (Pl. 1, F). Even here, between the nearly mature cystocarps, immature carpogonial branches and clusters of trichogynes may be seen as well as patches of male cells when the pustule is bisexual (fig. 2, f). The total number of carpogonial branches produced in a single pustule may be enormous.

At an early stage the carpogonial branch consists of a comparatively large flask-shaped carpogonium and a small cell borne laterally near the top of a rather large supporting cell which later may produce one or two short

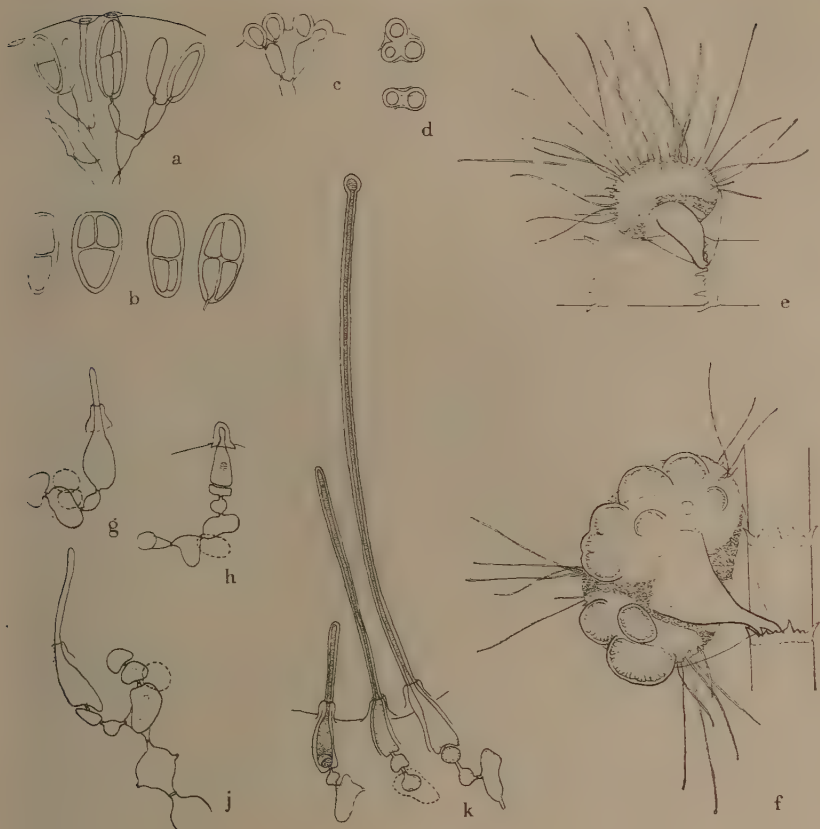


FIG. 2.—*Episporium*. Reproduction. a, b, asexual: a, small portion of surface of pustule showing stages in development of tetrasporangia and two empty sporangium walls; b, tetrasporangia. c, d, Male: c, side view showing mother cells with divergent spermatangia, spermatium escaping from one; d, surface view, one with two, the other with three spermatangia formed from each mother cell. e, f, Monocious pustules, ♂ areas deeply shaded: e, young pustule with very many trichogynes in all stages of development and a narrow band of spermatangia low down on the cushion; f, older pustule with many developing cystocarps, clusters of trichogynes and extensive male areas; base of central cell bifurcate before entering host tissues; g–k Female: g, young two-celled carpogonial branch attached laterally to bearing cell, two sterile branches on latter, one single-celled the other two-celled, trichogyne already emerging; h, slightly older but with shorter trichogyne, third cell just cut off from base of carpogonium; j, three-celled carpogonial branch fully formed, trichogyne elongating, sterile branches and relation of bearing cell to axial cells shown; k, group of female organs of varying ages showing development of trichogynes. e, f, $\times$ ca. 100, c, d, $\times$ 750, all other figures $\times$ 500.

sterile branches (fig. 2, g). As the trichogyne pierces the membrane and begins to elongate a second small cell is cut off from the base of the carpogonium and at the time of fertilization the carpogonial branch is always three-celled (fig. 2, h–k). Details of development immediately subsequent to fertilization have not yet been fully elucidated, but apparently the supporting cell itself

acts as an auxiliary cell. No sign of connecting filaments of any kind has been found, but an elongation of the base of the carpogonium towards the supporting cell has frequently been seen. Everything indicates that the carpogonial branch gives rise to a single cystocarp. Eventually large multinucleate fusion cells are formed from which repeatedly dichotomizing branches build up the more or less hemispherical cystocarp; at the ends of these the numerous carpospores are cut off. There is no cellular envelope, the cystocarp being protected only by the common membrane. A single pustule may produce a dozen or more cystocarps which project from its surface, giving it a curiously lumpy appearance (Pl. 1, F). The pustule sketched in fig. 2, f, bore numerous cystocarps, of which nine in varying stages of development, one apparently compound, are shown, clusters of long trichogynes and in addition extensive 'male' areas.

Discussion. Möbius ventured no opinion as to the systematic position of *Episporium*, contenting himself with pointing out that it was of a type otherwise unknown to algologists, and this still remains true. In his examination of cystocarpic material he records noticing in one instance a cell filament apparently connecting a developing cystocarp with a structure ending in a trichogyne, but adds that in no other instance did he observe any such structure. This isolated observation appears to have misled subsequent workers. The structure he observed might have been explained as being a trichogyne doubled back, as often happens, over a squashed female plant, but as shown in his figure (loc. cit. fig. 9), it is quite unlike anything found in *Episporium* and was probably some extraneous filament having nothing to do with the parasite—possibly a fungal hypha.

More misleading still, of course, is his interpretation of the organism as a cellular mass epiphytic on a tetrasporangium of *Centroceras*, which interpretation has obviously been accepted by the few other algologists who have examined the Australian material—Askenasy, probably Bornet, and certainly, from his own statement, Schmitz (1889, p. 2).

Möbius's description of the female organ is not clear:—"The Trichogyne often reaches considerable length and arises on two or three smaller cells, the Trichophor, which appears to arise from a larger carpogonial cell (fig. 7)." Askenasy (1888, p. 41), after describing the numerous trichogynes, the longest projecting about 160 μ beyond the membrane, continues:—"Unten schliesst sich an das Trichogyn ein dreizelliges Trichophor an" (which statement has apparently given rise to the belief that the carpogonial branch is four-celled), "das seitlich an einer grösseren Zelle mit dichtem Inhalt ansitzt die an ihrem oberen Theil noch eine kleine Zelle mit stark gequollener Wand trägt". This no doubt corresponds to one of the small sterile cells cut off from the bearing cell often observed in the South African material. It is less easy to interpret what is meant by his statement that in the ripe cystocarp "seitlich oder am Scheitel findet man bei ihnen manchmal 2 bis 3 fädig verbundene Zellen", unless he was referring to small portions of the inner rows of cells which had become displaced, as may often happen. But the "gewisse stumpfendigende zwei- bis dreisellige fädige, über die Gallerthülle des Thallus vorragende Aeste" shown in Möbius's fig. 8, which Askenasy thought played a part in the formation of the cystocarp, are certainly young carpogonial branches in which the trichogynes had not yet elongated. Askenasy assigned *Episporium* to the Cryptonemiaceae, stating that in so doing he was following Bornet, who seems to have examined the material and who held that, from consideration of the cystocarp, this was the natural systematic position.

Schmitz (1889), however, without stating his reasons for so doing, places *Episporium* among the Ceramiaceae, creating for it a new subfamily Episporiaceae, and subsequently (Schmitz & Hauptfleisch, 1897) gives a description of the

genus, in the course of which he describes the female organ as a four-celled curved carpogonial branch borne laterally on a somewhat enlarged basal cell which is itself borne on a normally two-celled dichotomy of a cell filament of the thallus. Schmitz (1889, pp. 2 & 18) explicitly states that he had himself examined the material of *Episporium*, but since he evidently accepts the interpretation of the central cell as an abnormal cell of the host, he too failed to recognize it as an integral part of the parasite.

More recently Mme. Feldmann (1947, p. 179), basing her argument on the description given by Möbius, concludes that *Episporium* cannot belong to the Ceramiaceae. As regards the development of the cystocarp, further investigation is still necessary, but her argument based on the type of germination obviously falls away entirely, since it in turn is based on the erroneous interpretation of the organism given by Möbius. On the contrary, the mode of development of the spore perhaps at present affords one of the strongest arguments in favour of inclusion in, or at any rate close relation to, the Ceramiaceae, since it most certainly approaches more nearly to the 'bipolar' type of germination described as characteristic of the Ceramiales alone among the Florideae (Fritsch, 1945, p. 607; Kylin, 1937, p. 106) and in general shows no resemblance to the more universal type where the initial divisions are longitudinal. A possible exception to this may perhaps be found in the aberrant cases referred to above, where the central cell divides giving rise to two lobes (fig. 1, p, q). As yet, however, very little is known about germination in parasitic Florideae, and where there is such a high degree of specialization, deviations from the normal are to be expected.

Thallus construction is on the whole extraordinarily regular. The structure of the cushion is closely comparable with types of construction found among both the Gigartinales and the Cryptonemiales, cf. *Endocladia*, but the presence of the large central cell at once distinguishes it from anything found in these orders and again suggests possible affinities with the Ceramiaceae.

But the carpogonial branch is certainly not four-celled and is unlike anything as yet described among the Ceramiales. On the other hand, long connecting filaments are conspicuous by their absence and apparently each cystocarp develops from an individual carpogonial branch, and when mature the superficial position and lack of cellular investment make it comparable with those of some of the more massive Ceramiaceae.

So far as affinity with the Choreocolacaceae* is concerned, apart from certain general resemblances such as position and structure of the cruciately divided tetrasporangia, *Episporium* has little in common with the algae included in that family. Thallus construction is fundamentally different as is the unique mode of attachment to the host, in both of which the large central cell plays a dominating role. But the carpogonial branch approaches most nearly in position and form to that of some members of the Choreocolacaceae, particularly *Choreocolax* and *Harveyella* (where however it is described as four-celled), although the mature cystocarp is very different both in position and structure.

Argument based on the fact that in the majority of Floridean parasites host and parasite are closely related is attractive but unfortunately not valid, since it is subject to too many exceptions, curiously enough in several cases where one of the partners is a member of the Ceramiaceae, as for instance, *Syringocolax* parasitic on *Gelidium*.

* Newton (1931, p. 423) gives Choreocolacaceae. Sturck (1899, p. 97) originally proposed Choreocolacaceae as a subfamily of Gigartinaceae; subsequently (1926, p. 602), without altering the form, he proposed it as a provisional family in the Gigartinales. Kylin (1927, p. 602) and Fritsch (1945, p. 650) retain Sturck's form but again with the rank of family. Since the form used by Newton conforms to modern usage for family names and is probably orthographically more correct, it is adopted here.

III. AILOCOLAX, gen. nov.

Some years ago (January 1944), while examining clumps of *Polysiphonia incompta* and an undetermined species of *Ophidocladus* at Muizenberg, a small polysiphonous alga recently described under the name of *Falkenbergiella caespitosa* (Pocock, 1953, p. 42) was found creeping among the larger algae. On some of its branches small pearly excrescences were noticed which, small as they were, were rendered conspicuous by their lack of pigment, contrasting sharply with the rather fuscous colour of the host. In freshly gathered material no cell walls could be distinguished and at first they were thought to be animal in nature, but on addition of a fixative, or even if left for a while, shrinkage of the protoplast took place, cell walls became apparent and the plant nature of the structures was evident. The minute rounded 'pearls' proved to be mature cystocarpic branches of a parasitic alga of an entirely new type. The curiously glistening effect of the parasite as contrasted with the dull colour of the host led to the choice of the generic name.*

Aiolocolax, gen. nov. (ἀιολος, bright, shining, and κολαξ, a parasite.)

Algae parasiticae minutissimae quarum thallus filamentum est tenue, ramosum, monosiphonum, inter siphonem centrale et cellulas pericentrales specierum *Falkenbergiellae* crescens.

Rami fertiles cellulis e filamento crescentibus formantur, quae cellulae inter cellulas hospitis pericentrales proveniunt, tum transversos se dividunt ita ut pars inferior cellulae stirps rami unicellularis fiat, pars superior cellulam rami apicalem formet, e qua oritur ordo cellularum axialis ramusculos brevissimos laterales in spiram dispositos producentium, tota structura quam maxime congesta.

Ramus asexualis sporangia multa producit, quae intus in polyspora divisa sunt.

Ramus mas spermatangia per totam superficiem apice excepto producit.

Ramus femineus procarpia compluria in textura sua defossa producit quorum trichogynae e superficie eminent: cystocarpium cellulis parvis circumdatum est, e superficie cellulis formatis sed nullus est murus certus nec ostiolum.

Aiolocolax pulchella, sp. nov. (Figs. 3 and 4; Pls. 2-4.)

In *Falkenbergiella caespitosa* parasitica nullam plerumque hypertrophiam hospitis efficit. Cellulae filamentorum endophyticorum multinucleatae sunt, in connexione protoplasmica cum cellulis centralibus hospitis. Rami fertiles permulti, cum iuvenes sunt fusiformes, in successione formati, aut aliquando in cristis densioribus.

Ramus asexualis multa sporangia in spiram disposita habet, quae intus in circa 32 Polyspora divisa sunt.

Ramus mas elongatus est, superfice spermatangiis co-operta.

Ramus femineus 5-12 procarpia habet cum trichogynis longis fere duplo latitudine rami longioribus: plerumque unum aut duo cystocarpia, interdum plura, unus quisque ramus format. Cum maturus est, ramus rotundatus est aut si plura cystocarpia formata sunt, in orbes rotundatus.

Aiolocolax, gen. nov.

Minute parasitic algae, the thallus a slender branched monosiphonous filament growing between the central siphon and the pericentral cells of species of *Falkenbergiella*.

Fertile branches produced by cells which grow out of the main filament, emerge between the pericentral cells of the host and then divide transversely; the lower part of the cell becomes the unicellular stalk of the branch, the smaller upper part forms the apical cell of a small branch-system: this consists of an axial row of cells bearing short lateral branchlets arranged spirally, the whole structure exceedingly congested.

The asexual branch produces many sporangia the contents of which are divided into polyspores.

* For this, as also for the generic name chosen for the following parasite, I am indebted to Professor Kenneth White of Rhodes University, Grahamstown.

The male branch bears spermatangia over the whole surface except the apex.

The female branch produces several procarps embedded in the tissue, the trichogynes of which project from the surface. The cystocarp is surrounded by small cells formed from the surface cells of the branch but there is no definite wall and no ostiole.

Aiolocolax pulchella, sp. nov.

Parasitic on *Falkenbergiella caespitosa* usually not causing any hypertrophy of the host. Cells of the endophytic filament multinucleate, in protoplasmic connection with the central cells of the host. Fertile branches numerous, fusiform when young, formed in succession or in fairly dense tufts.

Asexual branch with many sporangia arranged spirally, contents of each divided to form about 32 polyspores.

Male branch elongated, surface covered with spermatangia.

Female branch with 5-12 procarps, trichogynes long, about double the width of the branch in length; usually one or two cystocarps, sometimes several, develop on each branch. When mature rounded, or if several cystocarps are formed, with rounded lobes.

Asexual branch $101-118\ \mu \times 201-336\ \mu$; Polysporangia $31-39\ \mu \times 39-47\ \mu$

Young ♀ „ $72-118\ \mu \times 164-302\ \mu$; Trichogyne $69-160\ \mu$

Mature ♀ „ $134-202\ \mu \times 202-375\ \mu$; Cystocarp $130-200\ \mu \times 106-140\ \mu$

Carpospore $6-8\ \mu \times 19-22\ \mu$

Mature ♂ „ $61-119\ \mu \times 85-348\ \mu$

Occurrence. Parasitic on *Falkenbergiella caespitosa* growing on rock often partially sand covered, between tide marks or just below low-tide level, most often near the margins of reefs, on ledges or isolated boulders just awash at low water, or if higher up on the shore, growing among and protected by larger algae.

Geographical Distribution: Widespread on South African coasts, to be expected wherever the host is found; collected from Blaauwberg on the west coast to Embotyi near Lusikisiki on the east. Recorded from the following stations:

Western Province: Blaauwberg Strand (8180); Muizenberg (7832, 10387, 10820 Type, etc.); Strandfontein (9255); Kingfisher Creek, Sedgfield (9320); Storms River (8710); Jeffrey's Bay (8307); Laurie's Bay (8422); Witsands (11215).

Eastern Province: Richmond, Cannon Rocks, very abundant (7984); Kasouga, the Ship Rock (8245); Kowie, Salt Vlei (10168, etc.); Fish Point (8080, 8110); Waterloo Bay (8060); Morgan Bay (9384); Cape Morgan (9294); Embotyi (10195).

Type Locality: Muizenberg, rocks at foot of steps leading from the station to the beach.

Observations. After the first collection constant search was made and *Aiolocolax* has now been found at Muizenberg all the year round and all stages have been obtained. It is however more abundant on the east coast; at Cannon Rocks near Richmond in the Alexandria District peculiarly rich material has been collected and it is common at the Kowie. There seems to be no definite seasonal variation; all stages may be found at any season of the year, but at any one time one type of plant may be more abundant than the others. Considerable difficulty was experienced in finding a suitable fixative, since most of those in general use cause marked shrinkage within the limiting membrane of the external branch. On the whole, Neutral Formalin has given the best results. As in most parasitic Florideae, degeneration is accompanied by a darkening due in part at least to a transference of pigment from the cells of the host to those of the parasite; if kept unfixed for a time, the hyaline appearance changes, first to a pale pink, later to a darker colour, the colour change being accompanied by shrinkage of the protoplasmic contents of the cells.

The vegetative thallus consists of a sparingly branched, monosiphonous filament of elongated cells growing in the angle between the central siphon and two adjacent pericentral siphons of the host (fig. 3, a-f). There may be more than one such filament in one and the same branch each running parallel with the primary filament from which it has arisen and to which it is joined by a short transverse or oblique branch of one or more short cells; such connecting branches most often pass across between two successive central cells.

the only part external to the latter being these fertile branchlets. Among parasitic Florideae the only one in which a comparable habit has hitherto been described is *Choreonema*.

Most often the filament grows towards the apex of the infected branch, the initial cells of the fertile branches at first arising from it in sequence (Pl. 3, E), but later, growth may proceed in both directions from the point of infection (Pl. 3, A, F), probably as a result of the development of secondary filaments. Growth of the filament is apical, the apical cell being somewhat attenuated with denser granular protoplasm (fig. 3, f).

The somatic cells of the parasite are much narrower than those of the host and like them, are multinucleate; there are no chromoplasts and the response to stains is different. Consequently it is fairly easy to trace the course of the parasite within the host. Since the wall substance of *Falkenbergiella* is comparatively thick, there is sufficient space for the delicate parasitic filaments to penetrate between the siphons of the host without displacing them to any appreciable extent. Hence, in general, *Aiolocolax* causes no hypertrophy of the host. Where however growth of the parasite is particularly vigorous, parallel filaments are formed and secondary initials arise between the fertile branchlets of the first formed series, so that an accumulation of the internal parasite cells may result and cause some hypertrophy as the infection becomes heavier (Pl. 3, B, C), but such cases are comparatively rare; a contributory cause is the fact that the base of the cell giving rise to a fertile branchlet as well as the adjacent cells of the filament become very rich in cell contents and increase considerably in diameter, staining even more deeply than the other cells of the filament. With Aniline Blue in particular the difference between parasite and host is most marked. Owing to the absence of chromoplasts in the parasite cells the nuclei, with radiating protoplasmic strands, show remarkably clearly as deep blue star-shaped bodies suspended in the much more lightly stained cytoplasm (fig. 3, d).

As the parasite grows, its cells make contact by means of pit connections with those of the host; most frequently such connections are formed near the base of a central cell, but occasionally with pericentral cells. There is no penetration of the host cells by the parasite (fig. 3, f).

Both asexual and sexual plants of *Falkenbergiella* may be infected, although the former seem to be the more frequently attacked. If the host is a female plant even the cystocarps may be invaded by *Aiolocolax* (Pl. 2, B), the parasite growing freely between the two layers of the wall. In one such case numerous fertile branches were developing, some growing outwards, others inwards into the cavity of the maturing cystocarp. From this it may be inferred that the growth of the parasite is considerably more rapid than that of the host.

Development of the fertile branchlet is most characteristic. The initial cell may be one of the cells of the filament itself, or a cell cut off laterally, or the terminal cell of a short two- or three-celled lateral branch. It begins to lengthen in a direction perpendicular to the axis of the host, pushing outwards between two adjacent pericentral siphons, reaches the surface and begins to emerge pushing up the outer membrane as it does so. At first dome-shaped, it soon elongates more or less at right angles to the surface of the host, enclosed in a membrane which is continuous with but thinner than that of the host (fig. 3, a & b). Division soon begins. The first division is transverse, cutting off an apical cell from the large stalk cell (fig. 3, c); succeeding divisions may also at first be transverse but soon become oblique, the apical cell cutting off basal segments in spiral succession. Eventually it is dome-shaped outwards and a flattened pyramid towards the inside, apparently typically three-sided, although the number of cutting faces appears to be somewhat variable (fig. 3, e-g). Each segment proceeds to cut off one or more laterals, each of which functions as the apical cell of a small branch, while the remnant of the segment

becomes a unit of the central axis (fig. 3, f, g). Thus each fertile branchlet is actually a much congested branch system which when fully formed consists of a well-marked central axis of comparatively large cells surrounded by a close spiral of fertile laterals of limited growth. The latter are of varying length; some, particularly the first-formed basal branches, are short with a minimum of somatic cells, others are longer and may themselves branch once or twice. The cells of the main axis are very characteristic, multinucleate with well-developed broad pit connections; when the laterals branch each forms a subsidiary axis, more or less parallel with the main axis and formed of similar but smaller cells (fig. 3, h); hence in optical section large well-developed branchlets may at first sight appear multiaxial. This complicated structure is most easily followed in old asexual axes which have shed most of their polyspores.

Growth is continuous, the apical cell remaining clearly defined; branching of the fertile axis is rare but occurs from time to time, more frequently in the male plant. Occasionally it occurs early in development, more usually in older vigorous branchlets near the tip. The short, stout, unicellular stalk formed from the initial cell at its first division persists throughout the life of the branchlet; it enlarges considerably, the lower half remaining embedded in the host tissue, the upper half exposed. The protoplasts of the stalk cell and of the adjacent somewhat enlarged cells of the filamentous plant body are densely granular, contain very many nuclei and stain deeply.

In the asexual plant the very young branchlet is somewhat fusiform in shape (Pl. 2, A, C); older well-grown axes are usually more or less cylindrical with a conical apex (Pl. 2, D, F), and since the older polyspores at the base are shed while others are still being formed apically, the structure of the branchlet as a whole and the origin of the sporangia are best studied in such old axes (fig. 3, h; Pl. 2, F). The laterals cut off from the basal segments usually develop without branching, each producing a single sporangium. The lateral segment divides into two, the adaxial segment forming the sporangium mother cell which enlarges and divides horizontally, cutting off the large sporangial cell from the smaller stalk cell. The abaxial cell does not divide again but enlarges tangentially becoming multinucleate, as does the stalk cell, and constituting the single 'cover' cell, if that term is applicable here. Laterals cut off from succeeding segments may develop similarly or more usually may branch, once, twice or even three times; the initial cell of the lateral divides, cuts off an abaxial segment which again develops into a three-celled sporangial branch while the larger adaxial segment continues as the apical cell of a short branch, at each division giving rise to a sporangial initial outwards (occasionally more than one) and an axial cell inwards. Finally, the apical cell itself produces a sporangial branch. Thus each lateral cut off from a segment of the apical cell may give rise either to a single sporangial branch or to a short axis, itself branching once or twice, and at each branching giving rise to one or more sporangial branches towards the outside.

In a well-developed asexual axis viewed apically, the sporangia appear to form approximately six or seven rows, but although the spiral arrangement is clear, from the above description it is obvious that a definite arrangement of sporangia is not to be expected since any axial cell may give rise to an indefinite number.

The sporangium itself enlarges greatly; at first dome-shaped it soon becomes more or less tetrahedral, after which enlargement is rapid. The first two divisions are no doubt meiotic, but are followed by further divisions, probably usually three, in smaller later-formed sporangia by two only. Cleavage of the cytoplasm follows, commencing at the surface and extending inwards, sometimes beginning before nuclear division is complete; in immature polysporangia the segments may often be seen to be binucleate. Finally,

when fully developed, the polyspore is a large structure, somewhat flattened in the radial direction, composed of about 16 or 32 spores; each spore is wedge-shaped, uninucleate, the nucleus lying rather nearer to the outward polygonal face, the narrow inner end reaching nearly to the centre (fig. 3, 1; Pl. 2, E-G). A central cell such as is described by Setchell (1923, p. 394) in the polysporangium of *Gonimophyllum Skottisbergii* is apparently not formed in *Aiolocolax*; in some cases it was clear that cleavage did not extend across the centre but apparently the cytoplasmic remnant is not organized into a cell. No nucleus could be seen in it although the nuclei of the spores themselves were well stained. The mature polysporangia and their subtending cells cover the surface of the branchlet, the tangentially elongated cover cells separating the polysporangia from one another (fig. 3, j; Pl. 2, E).

In the male plant (Pl. 3 B-D) the structure of the fertile branchlet is simpler than in the asexual plant but its compound nature is superficially more obvious. Each segment cuts off a number of laterals which may themselves function as bearing cells producing spermatangium mother cells direct, or may branch repeatedly, each ultimate cell becoming a bearing cell. The bearing cell cuts off two cells towards the outside and each of these divides again. The resultant four cells are the spermatangium mother cells (fig. 4, a). At first the mother cell is long and narrow but as successive spermatangia are cut off it tends to become shorter and broader. There is however considerable variation in size (from $3 \times 6-8 \mu$ to as large as $5 \times 11 \mu$, fig. 4, b). The spermatangia are small ($2 \times 3.5-6 \mu$), pear shaped with apical nucleus; they are cut off by oblique walls in a spiral series as if from a three-(occasionally two-) sided apical; the primary series is followed by a succession of secondary series of spermatangia which remain in protoplasmic connection with the mother cell for some time. Eventually the spermatangium wall fuses with the outer membrane of the branchlet, a pore is formed and the spermatium, pointed end first, escapes. In preparations stained lightly with fast green a series of membranes one within the other, left as successive spermatia are liberated, can be traced. From a single mother cell as many as three series of spermatangia still *in situ* plus traces of three or four walls have been counted (fig. 4, b, c; Pl. 3, D).

Before abstriction of spermatangia commences the young male branchlet presents a most characteristic appearance, like a miniature pineapple. The whole surface shows a diamond pattern, each diamond formed by the deeply staining apices of four mother cells, while the diamonds themselves are arranged in groups indicating the underlying branch systems. As abstriction of spermatangia progresses the regularity of the pattern is lost; growth is continuous and additional mother cells are formed while abstriction of spermatangia increases rapidly. Eventually the whole surface, with the exception of the apical and stalk cells, is covered with a dense fur of spermatangia in every stage of development and spermatia in process of escape, overlying the closely packed palisade of mother cells.

As in the male, so also in the young female branchlet division into areas corresponding to the primary lateral branches shows clearly, but again is obscured as development proceeds. The proportion of somatic cells is higher than in either the asexual or male branchlet; the young female-axis is densely covered with uninucleate vegetative cells, among which the carpogonial branches develop. A single branchlet may show as many as a dozen trichogynes in various stages of development, projecting in all directions and reaching a length almost equal to that of the whole branchlet ($69-160 \mu$) (Pl. 3, F). A number may be fertilized and development of the cystocarps begins. Sometimes only one cystocarp develops on a branchlet, quite often two or even three may mature; sometimes two develop to normal size while one or more begin to mature but are undersized. In yet other cases two adjacent developing

cystocarps merge so that what appears externally to be one, is actually two enclosed in the same cellular envelope (Pl. 3, B, F; Pl. 4, A, P, G). Unusually elongated female branchlets proved on examination to contain a number of developing cystocarps, some probably abortive (Pl. 3, F).

Apparently each lateral may produce a single carpogonial branch. On the adaxial side of the lateral a cell is cut off which enlarges, becoming rich in cell contents and forming the bearing cell of the carpogonial branch. The axis continues to grow forming a row of somatic cells and from the fertile axial cell itself as well as the axial cells below it similar branches grow up enveloping the developing cystocarp and later forming a rudimentary wall around it. As a result the carpogonial branch is sunk in an investment of densely packed young cells, most richly developed on the abaxial side (Pl. 4, B-D).

The bearing cell cuts off two sterile cells on opposite sides, one of which, often but not invariably on the abaxial side, later divides into two. From the apex of the bearing cell the carpogonial initial is cut off and begins to enlarge. At first it is broadly conical with the short neck just touching the outer membrane (fig. 4, e) and the broad base close to the bearing cell. Enlargement follows and from the base of the carpogonial initial three small cells are cut off in succession, the first, adjacent to the bearing cell, slightly larger than the other two (fig. 4, f-j). The four-celled carpogonial branch thus formed has a very characteristic form which changes considerably as development continues. After the three small cells have been cut off the carpogone elongates in both directions. Towards the outside it becomes bottle-necked, forming the young trichogyne which pushes up the membrane of the branchlet while the lower end elongates downwards towards the bearing cell, displacing the row of small cells so that the uppermost appears to have arisen laterally on the carpogone (fig. 4, k and l). Elongation of the trichogyne is probably preceded by a fourth nuclear division but the presence of a nucleus in the trichogyne has not been established; it elongates, emerging through a pore formed in the apex of the projecting membrane (fig. 4, m, n; Pl. 3, H). When ready for fertilization the female apparatus thus consists of eight cells plus trichogyne:—bearing cell with two sterile branches, one two-, the other one-celled, and a four-celled carpogonial branch with a long trichogyne (fig. 4, m; Pl. 3, G, H). With fast green there is differential staining: the bearing cell and its branches stain deeply, the carpogonium less so, but the large nucleus in its base shows clearly; the three small cells stain very lightly, as does the trichogyne, the wall of which stains a characteristic very light blue. The protoplast of the trichogyne is slightly granular and the tip usually swollen. Reception of the spermatium may apparently be either lateral or terminal; the two walls are absorbed at the point of contact and the protoplast of the trichogyne concentrates towards the spermatium (fig. 4, o).

No distinct auxiliary cell is formed, the bearing cell itself functioning as an auxiliary cell. Union between it and the carpogonium has not been seen (with one possible exception), but the outgrowth of the carpogonium towards the bearing cell, the protuberance which can sometimes be seen formed at the upper end of the latter towards the carpogonium, and its behaviour after fertilization all indicate that it performs the function of an auxiliary cell. Actual union between it and the carpogonium must be very fleeting, since numbers of carpogonial branches in all stages have been examined. After fertilization the rapid growth of the enveloping filaments soon displaces the carpogonial branch from its proximity to the bearing cell; its remains may often be traced in the rudimentary ostiole of developing cystocarps at a comparatively late stage (Pl. 4, E, G).

Immediately after fertilization the bearing cell begins to enlarge, and sometimes two types of nuclei can be distinguished in it, a larger one, presumably the diploid nucleus, in the upper portion, and near the base a smaller

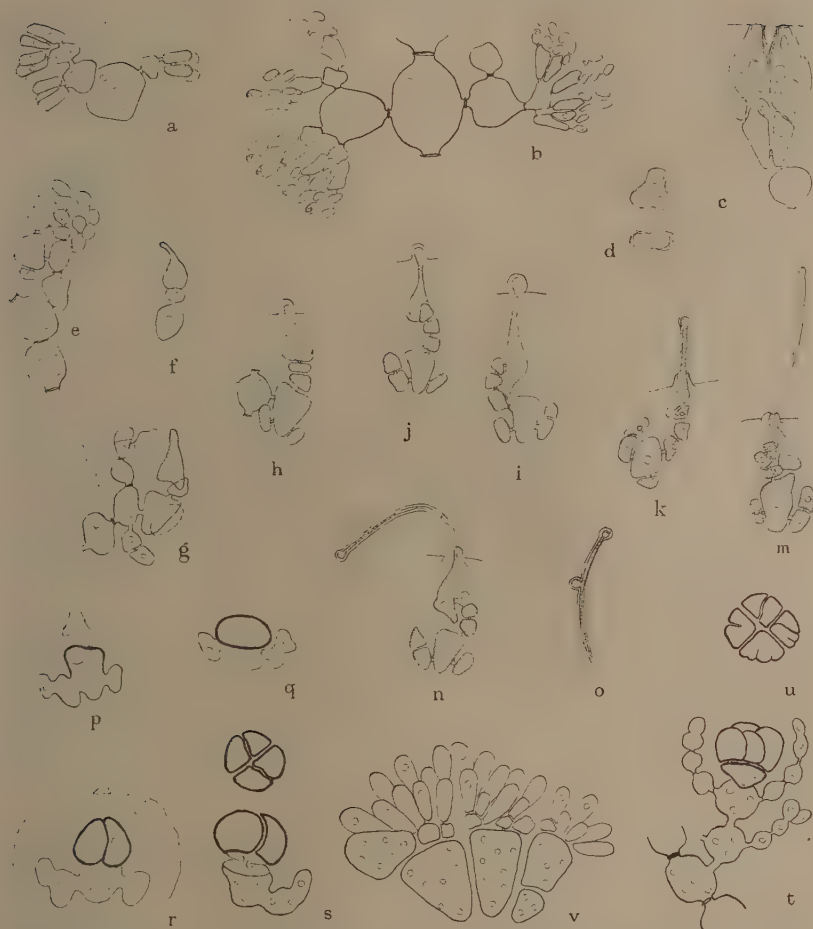


FIG. 4.—*Aiolocolax*. Sexual Reproduction. a-d, Male: a, axial cell with cells bearing spermatangium mother-cells; b, axial cell with two laterals each producing bearing cells, spermatangia developing from mother cells; c, two mother cells *in situ* stained with Fast Green to show walls; d, groups of spermatangia, produced two or three per mother cell, surface view. e-o, Female: e, bearing cell *in situ* with initial cell of carpogonial branch and one sterile cell, showing relation to adjacent somatic cells; f, first cell of carpogonial branch cut off; g, preparation for cutting off of second cell; h, third cell about to be cut off; j, female apparatus complete, consisting of four-celled carpogonial branch, bearing cell and two sterile branches, one two- the other one-celled; k, l, elongation of base of carpogonium, in l nearly complete with uppermost cell apparently attached dorsally to the carpogonium; m, n, trichogyne elongated ready for fertilization; in m, bearing cell is producing a protuberance towards the carpogonium; o, trichogyne with spermatium attached. p-v. Development of the carposporophyte; p, immediately after fertilization, diploid nucleus in upper part of bearing cell, lower part beginning to fuse with sterile branches, remains of carpogonium above; q, diploid cell cut off, fusion cell multinucleate; r, first division in diploid cell, above remains of carpogonium, outline of developing envelope indicated; s, later stage; above, surface view of four celled carposporophyte; t, young sporophyte *in situ* showing developing cell rows of the envelope; u, surface view of same; v, group of coenocytic cells and carpospores from a nearly mature cystocarp. c, d, $\times 750$; other figures all $\times$ ca. 500.

one similar to those in the lateral cells. A transverse wall cuts off the upper half and it begins to divide. The first two divisions are longitudinal and at right angles to one another, resulting in a group of four cells (fig. 4, p-s), and apparently the next few divisions are also mainly longitudinal (fig. 4, t, u). Meanwhile the connections between the base of the bearing cell and the three lateral cells widen, the nuclei multiply and the large fusion cell begins to form (fig. 4, p). Subsequent stages have not been followed in detail but eventually in the nearly mature cystocarp there is a very large basal coenocytic cell and above it a number of smaller coenocytes. From the upper surface of the latter arise short filaments from which the numerous small carpospores are abstracted by successive oblique divisions (fig. 4, v). When mature the carpospore is elongated, pear shaped and slightly asymmetric with a large central nucleus.

Meanwhile the somatic branches which begin to arise from adjacent axial cells at a very early stage continue to grow and form a somewhat ill-defined but well-developed wall of two or three layers of uninucleate cells around the developing cystocarp. There appear to be initially four groups of these branches, one adaxial, one abaxial and two lateral to the cystocarp. Optical section shows them converging over the top of the cystocarp, between them the remains of the carpogonium and the three small cells carried away from the bearing cell by the rapid growth of the carposporophyte and wall (fig. 4, p, r; Pl. 4, E, G). This is obviously a rudimentary pore but later becomes more or less obliterated; no definite ostiole is organized and in the mature cystocarp no pore is recognizable.

If, as sometimes happens, only one cystocarp develops in a branchlet it eventually comes to constitute nearly the whole of the branchlet, which is consequently almost spherical in shape; if two or more develop the branchlet becomes lobed, each lobe indicating either a single cystocarp or a composite one formed by two or even more cystocarps adjacent to one another becoming confluent and protected by a common envelop (Pl. 4, A, G-F). Occasionally cystocarp formation in a branch is delayed and the lower part is more or less cylindrical with one or more cystocarps forming rounded lobes at the upper end (Pl. 3, F).

Discussion. Here again, the affinities of this very individual parasite are not clear. As regards structure of the thallus as a whole, viz. branched monosiphonous filaments within and nothing but the fertile axes external to the host, it is obviously highly specialized in relation to the parasitic habit. The construction of the latter however may be helpful in consideration of possible relationships. The uniaxial structure derived ultimately from *oblique* segmentation of a large apical cell, the origin of the lateral branches from the axial cells and their structure and mode of branching all seem most nearly comparable with certain of the Cryptonemiales, in particular that somewhat aberrant member *Endocladia* (cf. Fritsch, fig. 166, C, G), although similar types of construction also occur among the Rhodymeniales.

Connected with the vegetative structure is the nature and mode of origin of the cystocarp wall, the development of which begins before fertilization. According to the account given by Phillips (1924, p. 557, fig. 8) a somewhat comparable structure is found in *Spyridia filamentosa* where the specialized lateral branches show a close similarity as regards somatic organization and origin of cystocarp wall. But in Phillips's opinion (l.c., p. 559-60) it is doubtful whether *Spyridia* should be included in the Ceramiaceae, where as a rule the cystocarp is destitute of a wall. On the other hand, cystocarp walls among the Cryptonemiales and Rhodymeniales (e.g. Champiaceae) may develop somewhat similarly. In the latter case moreover the cystocarp may be devoid of a pore (cf. Fritsch, p. 681).

The male organs show certain resemblances to those of the Choreocolacaceae. Sturch (1899, p. 90, Pl. III, fig. 5; 1924, p. 599, fig. 20) found in *Harveyella*

mirabilis two, three or more series of spermatangia cut off by alternate oblique divisions, in *Choreocolax polysiphoniae* (1926, p. 599, fig. 19) apparently many, again cut off obliquely and in *Holmsella pachyderma* (1924, p. 37, figs. 18, 19) a number produced singly by transverse division. According to Grubb (1925, p. 253 et seq.) abstriction of spermatangia by oblique subterminal walls is the general rule and often the first series is followed by a second and even a third; an indefinite number however is rare but characterizes *Endocladia* and apparently is also found among the Choreocolacaceae.

As regards the female reproductive apparatus its structure strongly suggests affinities with the Ceramiales, since the procarp with its four-celled carpogonial branch borne on the large bearing cell (but subterminally, not laterally), which also produces two groups of 'sterile' cells, one single- the other two-celled, appears very similar to that of the Rhodomelaceae. But subsequent development is different—the absence of a specialized auxiliary cell and the participation of the 'sterile' cells as well as the bearing cell in the formation of the fusion cell are features found in members of the Choreocolacaceae, especially *Harveyella*; early stages in post-fertilization development resemble those found in that genus, although later stages are very different, though less so from *Choreocolax* itself. In both those genera too the carpogonial branch is four-celled.

The sporangium unfortunately is not particularly helpful in a consideration of the systematic position. The single large 'cover cell' appears to be unique, but polyspores occur in diverse groups; they are of most common occurrence among the Ceramiales where a very similar type has been described by Setchell (1923, p. 394), in *Gonimophyllum Skottsbergii*; they are also known among the Rhodymeniales, e.g. *Chylocladia* (cf. Fritsch, 1947, p. 729) and *Coeloseira* (Hollenberg, 1940, p. 871).

Aiolocolax thus shows resemblances on the one hand to the Cryptomeniales and on the other to the Ceramiales. In some respects it shows affinity with the Choreocolacaceae, although it is certainly not closely allied to that family.

IV. ONYCHOCOLAX, gen. nov.

The discovery of *Aiolocolax* stimulated interest in parasites, especially of the Rhodomelaceae, and search was made for other small seaweeds of this kind. As yet, apart from *Episporium*, only one more has been discovered, growing on one of the commonest of the South African species of *Polysiphonia*, *P. incompta*. Although the host is much larger in every way than *Falkenbergiella caespitosa*, the parasite is even smaller than *Aiolocolax*, and owing mainly to the discrepancy in size between host and parasite is peculiarly difficult to detect. The fertile branch of the female plant normally bears two curved claw-like appendages and the generic name was chosen as descriptive of this feature.

Onychocolax, gen. nov. (ὄνυχ, a claw, talon.)

Algae microscopicae specibus Polysiphoniae parasiticae. Thallus filamentosus, monosiphonous, multum ramosus, inter siphonem hospitis centralem et cellulas pericentrales crescit, et inter cellulas ad iacentes siphonis centralis ramificat; nulla pars hospita externa est nisi breves axes fertiles qui ex hospite proveniunt inter cellulae pericentrales, praecipue ad segmentorum juncturas.

Axes mares et asexuales plerumque simplices sunt, interdum ramosi, axis femineus bifurcatus; trichoblastae absunt nisi in thallo femineo ubi apex ramusculi utriusque brevi trichoblasta terminatur cuius cellula apicalis elongata est, pilum unum aut alterum quasi unguiculum ferens.

Axes feminei bina procarpia plerumque ferunt, unum ad trichoblastae utriusque latus adaxiale. Quaterna sunt segmentis tetrasporangia, quae intus tetrahedraliter divisa sunt.

Onychocolax polysiphoniae, sp. nov. (Figs. 5, 6; Pls. 5, 6.)

Polysiphoniae incomptae parasitica multum hospita hypertrophiam efficiens. Axes fertiles cristis plerumque densis inter segmentis hospita surgentes; stirps elongata est, plerumque simplex, nonnumquam transverse divisa; parte inferiore subhospitis superficie latente, parte superiore eminente.

Axis asexualis polysiphonous cum 4 cellulis pericentralibus stichidium unicum formans cum sporangiis ordinibus 4 directis collocatis; si axis ramosus est, stichidium minus regulare.

Axis mas plerumque ramusculum unum antheridiale unicum formans, bifurcatus aliquando aut etiam in ramusculos complures divisus, omnes spermatangia ferentes.

Axis femineus ut in genera supra descriptus, pilis unguiformibus praecipue notabilis; procarpia trichogyna pilis brevior et propeos eminentes. Cystocarpium unum, aliquando duo, grandius, muro duplici, ostiolo bene definito; ex nasi quasi racemus carpospororum grandiorum pyriformium crescit.

Onychocolax, gen. nov.

Microscopic algae parasitic on species of *Polysiphonia*. Thallus filamentous, monosiphonous, much branched, growing between the central siphon and the pericentral cells of the host and spreading between adjacent cells of the central siphon; no part external to the host except the short fertile axes which issue from the host between the pericentral cells, especially at the joints between segments.

Male and asexual axes most often simple, sometimes branched, female axis regularly bifurcate; trichoblasts absent except in the female plant where the apex of each branchlet ends in a short trichoblast the apical cell of which is elongated and bears one or two claw-like hairs.

Female axis usually bears two procarps one on the adaxial side of each trichoblast. Tetrasporangia four per segment, contents divided tetrahedrally.

Onychocolax polysiphoniae, sp. nov.

Parasitic on *Polysiphonia incompta* causing considerable hypertrophy of the host. Fertile axes usually arising in dense tufts between segments of the host; stalk an elongated cell, usually undivided, occasionally divided transversely; lower part within the host tissues, upper part projecting from the surface.

Asexual axis polysiphonous, pericentral cells four, forming a single stichidium with sporangia in four straight rows; if branched, then stichidium less regular.

Male axis usually developing into a single antheridial branch, sometimes bifurcate or even divided into several branchlets, the whole producing spermatangia.

Female axis as described above for the genus, particularly notable for the claw-like hairs; trichogyne of the procarp shorter than the hairs and projecting near them. Cystocarp one, occasionally two, comparatively large; wall two-layered, ostiole well defined; from the base grows a bunch of fairly large pyriform carpospores.

Asexual branch $58-185\ \mu \times 103-280\ \mu$; Tetraspore $20\ \mu$

♂ „ „ $43-132\ \mu \times 86-264\ \mu$

♀ „ „ young $70-91\ \mu \times 105-116\ \mu$; Trichogyne $51-83\ \mu$; Claw $41-82\ \mu$

♀ „ „ mature $201-252\ \mu \times 185-268\ \mu$

Cystocarp $134-186\ \mu \times 185-268\ \mu$; Carpospore $12-16\ \mu \times 27-37\ \mu$

Occurrence. Parasitic on *Polysiphonia incompta* growing on rock in wave swept gullies and pools.

Geographical Distribution: As yet found only at a few stations on the east coast although the host is widespread. Difficult to detect and probably more abundant than would appear. Recorded from the following localities: Richmond, the Canon Rocks (7990); Kasouga, the Ship Rock (8160, 8408); Kowie, beyond Salt Vlei (8870, 10170 Type); Riet River, the Three Sisters: Kleinemonde (9104). Type Locality: The Kowie, beyond Salt Vlei.

Observations. Although the individual branches of *Onychocolax* are even smaller than those of *Aiolocolax* they are usually massed together in large numbers and this, together with the fact that they cause hypertrophy in the host, makes it just possible to pick out infected branches with the naked eye. Nevertheless it is probably often overlooked; once it has been found on a

plant of *Polysiphonia*, the infection usually proves to be general throughout the clump, though by no means all the branches are infected. So much material of *P. incompta* from the Western Province has been examined in vain for any trace of the parasite that it seems probable that it is confined to the warmer waters of the east coast. Further search will no doubt extend its range, possibly to Natal.

The form of the thallus is essentially similar to that of *Aiolocolax*, in that it consists of branched monosiphonous filaments within the host, giving rise externally only to fertile axes, but it differs from the latter in several important respects. As in *Aiolocolax* the primary parasitic filament lies in the angle made by the central siphon and adjacent pericentral cells of the host; the filament in a segment may consist of a single cell equal in length to those of the host and attached to the central cell near its base; more frequently each section consists of one long and one shorter cell, or of two or more short cells. At the end of the segment copious branching takes place resulting in a number of short, often broad and somewhat irregular cells which spread out in the space between the adjacent host segments, forming a kind of cap over the end of the lower segment. Some of these cells themselves emerge to form the initial cells of fertile axes, or they may give rise to other cells which so function (fig. 5, l). Thus at each node a number of fertile axes are formed, growing more or less perpendicular to the host in all directions (Pl. 6 A-D). Other branches of the nodal cap elongate and continue growth up into the next segment, while yet others turn back into the lower segment, growing down it and giving off branch initials towards the outside; consequently in older infections fertile axes may emerge between the pericentral cells all along the segment. This, combined with crowding due to the enlargement of the fertile axes, may result in the infected part being covered entirely by the parasite (Pl. 5, D, H). In such cases the mass of internal filaments may cause considerable hypertrophy. Further, should growth of the parasite be more active on one side of the infected branch, it may be bent to one side forming a very characteristic knee-shaped bend.

The first stages in development are the same in all three types of fertile axes (fig. 5, a-c). The initial cell grows out towards the surface and emerges from the host whose outer wall becomes continuous with that of the developing branchlet. The conspicuous membrane, which at first encloses the external part of the initial cell and subsequently the whole of the fertile axis, thus appears to be continuous with the outer wall of the host, while the lower part of the stalk cell within the host remains thin-walled. So close is the union between parasite and host membrane that it is often nearly impossible to detect the join (fig. 5, a, b, etc. and fig. 6, b). The cell elongates and divides transversely to form an apical cell and a larger lower cell which enlarges still further to form the characteristic unicellular stalk of the fertile axis; very occasionally a later transverse division results in a two-celled stalk.

The behaviour of the apical cell varies: it may continue to divide transversely to form a short unbranched axis, as is most often the case in tetrasporic and male axes, or it may give rise by two successive divisions to two apical cells, each of which develops into a short branch. This is almost invariably the case in the female plant, occurs occasionally in the male and still less often in the asexual.

The asexual or tetrasporic axis is typically simple, the whole forming a single stichidium; each segment cuts off four pericentral cells, all of which are fertile, so that there are four rows of tetraspores; occasionally the basal segment of the stichidium does not form tetraspores, or if it does, only one or two are formed (Pl. 5, A, B). When branching takes place the lower parts of the two branches frequently coalesce, so that a massive structure with tetraspores in whorls of more than four results; the upper parts may separate

and growth be continued as two branches, each with quadrate symmetry (Pl. 5, C). The tetrasporangium is divided tetrahedrally; the stalk cell widens tangentially and the abaxial cell divides longitudinally to form two rather large, oblong, slightly divergent cover cells.

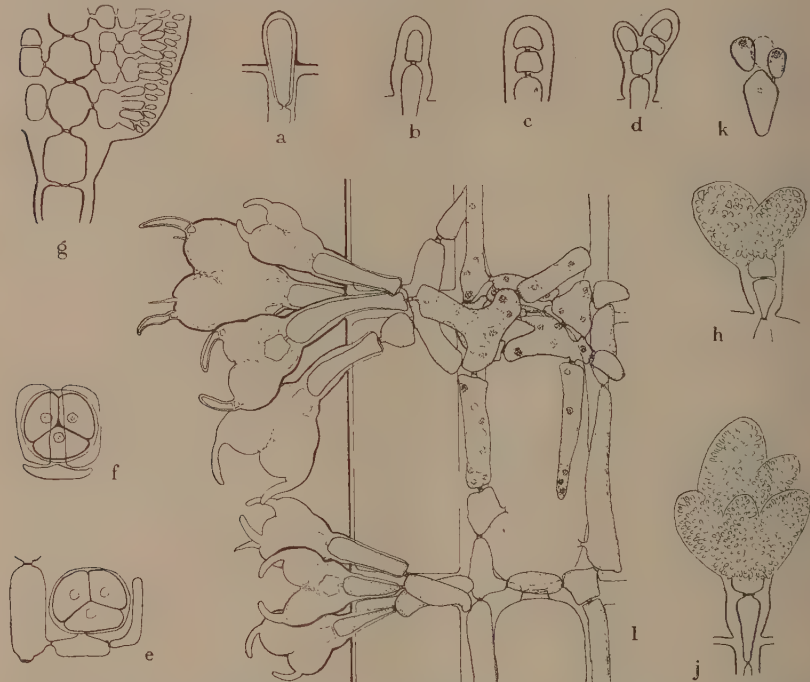


FIG. 5.—*Onychocolax Polysiphoniae*. a-d. Development of fertile axis: a, initial cell emerging; b, apical cell cut off transversely; c, first apical cell cut off from basal cell; d, two-celled branch formed by first apical cell pushed aside by second apical cell cut off from basal cell. e, f. Asexual reproduction: Tetrasporangium, e, in side view, f, surface view showing two large cover cells. Sexual reproduction. g-k, Male: g, base of male axis showing top of stalk cell, axial cells bearing pericentral cells (two divided), spermatangium mother cells borne directly on pericentral cells at base, above on bearing cells cut off from the pericentral cells; h, mature male axis showing bifurcation, and j, showing multiple branching; k, spermatangium mother cell with three spermatangia cut off obliquely. l, Female: part of pustule showing filamentous thallus between pericentral cells and central siphon, plexus of broader cells at end of segment, and two clusters of young axes emerging between segments; cell contents indicated in some cells of the thallus. h, j, l $\times 150$; k $\times 750$; other figures $\times 500$.

The male axis also is most frequently simple (Pl. 5, E, F), but branching occurs more often than in the asexual plant; whereas many pustules show no sign of branching, in others the majority of the axes may be branched. Bifurcation is the most usual form and may be primary as in the female axis or may occur later in development; occasionally repeated branching may take place (fig. 5, h, j). The number of segments cut off by the apical cell varies, but is usually from five to seven; the first, the basal cell, is larger than succeeding segments and may or may not cut off pericentral cells. It may remain bare and exposed or be partially hidden by downward growth from the segments next above (Pl. 5, E, F). Succeeding segments each cut off four pericentral cells which may themselves bear spermatangium mother

cells, particularly near the base, but more usually cut off secondary series of cells which function as bearing cells. Further, the pericentral cells occasionally divide transversely into two or three cells. Each spermatangium mother cell gives rise by oblique divisions to three, more rarely two primary subterminal spermatangia (Pl. 5, F). Apparently a secondary series may follow, but not more. When fully formed each spermatangium is broadly oval with apical nucleus and large central vacuole (fig. 5, k); as it separates from the mother cell a delicate protoplasmic strand connects the two for a time. Eventually, the spermatium escapes and passes out through the enveloping membrane of the axis, becoming narrower and more pointed as it does so, while the vacuole more or less disappears; as it escapes the protoplast appears densely granular and stains deeply.

The mature male axis is more or less fusiform with a comparatively long stalk; the whole surface with the exception of a very small apical cell and sometimes the basal cell is covered with spermatangia in various stages of development. When the axis is branched a more irregular and massive structure results unless the branching is at the base, when the two separate branches resemble the simple unbranched axis.

The young female axis is much the most distinctive feature of the whole plant and it is its characteristic appearance, rather like a small crab with outstretched claws, which inspired the choice of the generic name (fig. 5 l; Pl. 6, A-D). Here the young apical cell divides transversely and the upper cell forms the apical cell of a short branch; it is pushed to one side by enlargement of the lower cell (the basal cell) and a second apical cell is cut off on the other side. Each apical cell gives rise by transverse divisions to a short branch of from four to six or seven, but most frequently five cells. Of these, the first two are the largest and immediately cut off four pericentral cells; the second is the fertile segment and the fertile pericentral cell, the last cut off, is on the adaxial side. The third segment is smaller and may also cut off pericentral cells, but this may be delayed, incomplete or entirely omitted (fig. 6, a-d). Very occasionally a fourth segment with pericentrals may be formed, but in general after the third segment the rest of the branch is monosiphonous consisting from one to three cells; the terminal cell elongates developing into a somewhat thick walled, stiff, bristle-like structure, the claw. The claws of the two branches of the axis incline towards one another giving the crab-like effect mentioned above. Sometimes a second claw grows out from the end cell, or terminal and subterminal cells both form claws while in yet other cases both these developments take place in one and the same branch resulting in three claws inclined at various angles to one another (fig. 6, f-h, l). Meanwhile the basal cell from which the two apicals originated has enlarged and usually has cut off pericentral cells. Sometimes the complete number of four, two lateral and one each on the front and back, is formed; frequently only the lateral pericentral cells are cut off, while in yet other cases only a single one is formed or even none at all.

When ready for fertilization the slightly flattened female axis (fig. 6, h) presents a most individual appearance: the stout unicellular stalk bears a large basal cell, from which arise the two branches, apparently of the nature of unbranched trichoblasts. The two procarpis lie close to each other in the middle of the structure, their developing walls merging into one another at the base. Their trichogynes emerge close to the bases of the claws and lie more or less parallel with them. Formation of procarp and wall begin simultaneously, although at the time of fertilization the wall is still incomplete. The mature procarp is borne on the enlarged axial cell of the fertile segment which is early distinguished from adjacent axial cells by its shape (fig. 6, f, j, m-o), like a conical flask; even at a late stage in development it is still recognizable (Pl. 6, E). The bearing cell of the procarp is attached to it near the base; on its adaxial side is the two-celled sterile branch and above

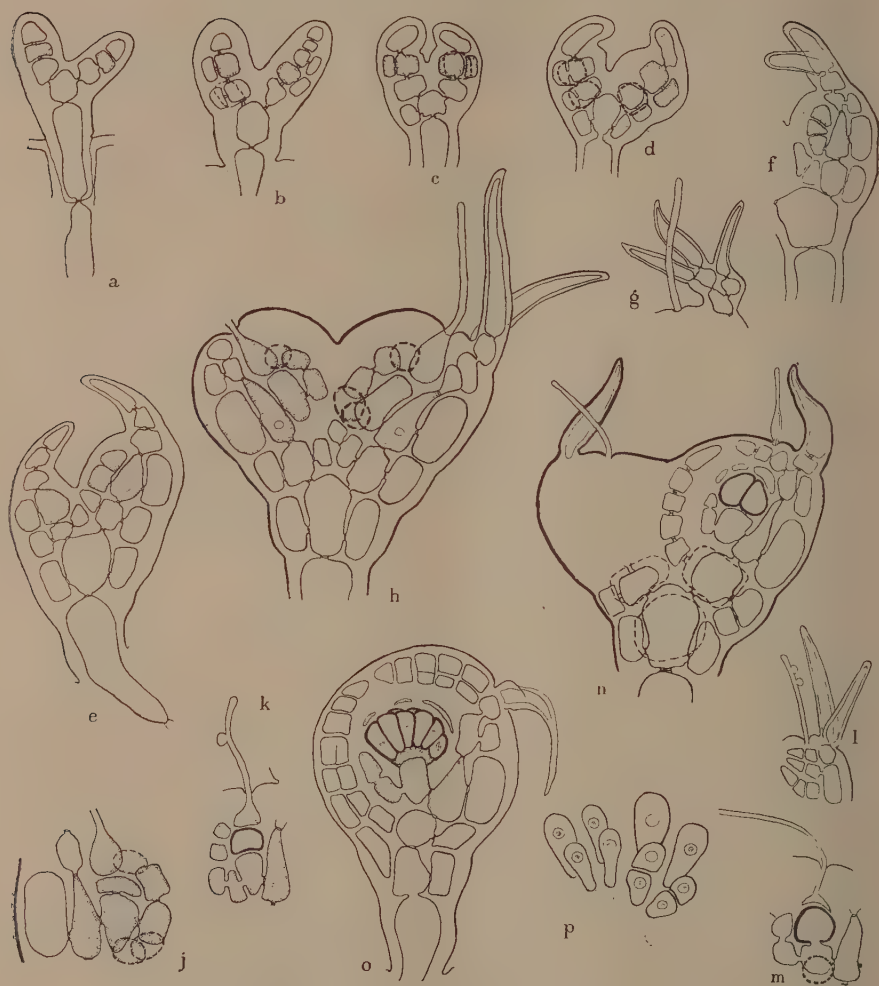


FIG. 6.—*Onychocolax*. Female. a-d. Development of fertile segment : a, both branches three-celled ; b, one branch five-celled, the other three-celled, cutting off of pericentral cells commencing ; c, d, preparing to cut off bearing cell ; e, f. Development of carposporophyte : in e, one branch of the axis much more strongly developed than the other, carposporophyte two-celled, in f, only one branch shown, carposporophyte three-celled, two 'claws' developing at apex ; g, apex with three claws ; h, female axis with fully formed carposporophytes, in the one on the right the bearing cell is enlarging in preparation for cutting off of the auxiliary cell ; axial cell of the fertile segment has assumed its characteristic shape. j-p. Development of carposporophyte : j, auxiliary cell cut off ; k, diploid cell enlarging, spermatium wall attached to trichogyne ; l, apex with two claws, two spermatia on trichogyne ; m, trichogyne withering, enlargement of diploid cell advancing ; n, beginning of division ; part played by adjacent segments in formation of wall shown ; o, division further advanced, wall cells cutting off pericentral cells on the outside, remains of carposporophyte branch still seen ; p, group of carpospores squashed out of nearly mature cystocarp. All $\times 500$.

this the carpogonial branch ending in the flask-shaped carpogonium which lies immediately above the bearing cell. The uppermost of the three small cell lies in a different plane from the other cells of the carpogonial branch. Below the bearing cell it is sometimes possible to distinguish a third sterile cell, but apparently this is not always formed, or possibly not until a later stage (fig. 6, m). By this time the filaments forming the cystocarp wall are already forming, those from the pericentral cells of the first segment developing earliest; in addition to the pericentral cells of the fertile segment itself, the adaxial pericentral cell of the third segment may also take part in the formation of the wall, although this is apparently not always the case. Later in development each cell of the wall cuts off two pericentral cells on the outer side, thus forming the outer layer of the wall in the usual way (fig. 6, n, o).

The trichogynes are shorter than the claws which appear to protect them and possibly aid in fertilization by directing the spermatia into the space between them in which the two trichogynes are enclosed. As development of the carposporophyte proceeds the claws are shed and the trichogynes shrivel, though traces of them may persist for some time.

After the union of the spermatium with the trichogyne the bearing cell, which has grown up towards the base of the carpogonium, cuts off a large auxiliary cell (fig. 6, h & j). As the auxiliary cell enlarges subsequent to fertilization the pit connections between the bearing cell and sterile cells are seen to be widening in preparation for the formation of the fusion cell (fig. 6, k, m), although the identity of each can be traced after division in the young carposporophyte is well advanced, while the remains of the carpogonial branch also survive for some time (fig. 6, n, o).

Occasionally one of the primary branches bifurcates again, each arm producing a fertile segment; in such cases all three procarps may develop, be fertilized and begin to produce cystocarps (Pl. 6, F). Very rarely two successive segments may be fertile and form procarps. On the other hand, it is not unusual to find cases in which the development of the two branches of the female axis is unequal (fig. 6, e), while in yet others one branch only is formed or the second branch is abortive and all trace of it disappears early in development (fig. 6, o); but on the whole the dual structure of the female axis is remarkably constant and normally both carpogonia are fertilized and both carposporophytes begin to develop. In general however only one reaches maturity, each axis producing a single cystocarp which eventually constitutes nearly the whole of the axis. It is urn-shaped with a two-layered wall and well-defined ostiole; the pear-shaped carpospores are larger and less numerous than in *Aiolocolax* (fig. 6, p; Pl. 5, H, J).

Discussion. In this case, unlike the two preceding, there can be no doubt as to the suborder of the Florideae in which *Onychocolax* should be placed, even lacking complete details of procarp development, it clearly belongs among the Ceramiales. The slight suggestion of sympodial branching makes it necessary to consider a possible affinity with Dasyaceae, but there the cystocarp wall begins to develop subsequent to fertilization, whereas in *Onychocolax* it is already well advanced even before the procarp is fully formed. The apparent sympodial nature of the branching in the female axis is probably due to the greatly congested habit. The polysiphonous structure of the fertile axes, nature of the reproductive organs and particularly of the cystocarp all indicate that it belongs to the Rhodomelaceae but to which subfamily is not so clear. According to Falkenberg's classification (1901, p. 533) there are only two possible sections to which it might belong—Lophothaliae and Bostrychiae, in both of which there is a verticillate arrangement of the sporangia. The latter however is characterized by the regular subdivision of the pericentral cells; in *Onychocolax* such division may certainly occur in the male axis but

even there is not of regular occurrence. The Lophothaliae on the other hand have undivided pericentral cells but are characterized by the persistent, pigmented monosiphonous branches which may become polysiphonous at the base. In *Murrayella pericladus* these branches are very characteristic, consisting of a fairly long monosiphonous branch with several polysiphonous segments at the base; the individual branches of the female axis of *Onychocolax* can well be interpreted as of the same nature rather than typical trichoblasts. Further, in *Murrayella* there are four pericentral cells and four sporangia per segment. In the Lophurellae where there are also four pericentral cells, in the fertile segment of the female branch five are formed, but the fact that in *Onychocolax* the fertile segment like other polysiphonous segments has only four pericentral cells, though exceptional among the Rhodomelaceae, is not unknown since it has been reported for *Laurencia*. The participation of the segment next above the fertile segment in the formation of the cystocarp wall suggests a possible affinity with the Rhodomelaeae, but may apparently occur in other groups. Details of wall formation among the Lophothaliae have unfortunately not been available.

In many ways *Onychocolax* resembles *Colacopsis Lophurellae* described by Kylin (1919, p. 61) from South America and the Falklands and placed by him among the Bostrychiae. This species is however imperfectly known and there is no information as to the nature of the part of the parasite within the host; apparently as in *Onychocolax* the only parts external to the host are the fertile branches, but these are very different in the two algae.

On the whole a place among the Lophothaliae, Subfamily VII of the Rhodomelaceae (De Toni, 1903, p. 1007) seems to be indicated for *Onychocolax* which is therefore provisionally assigned to that sub-family.

GENERAL DISCUSSION AND CONCLUSION.

The four parasitic algae here concerned form an interesting little assemblage characterized by minute size, marked reduction and highly specialized thallus construction, representing the extreme results of adaptation to the parasitic mode of life. In three of them, *Choreonema*, *Aiolocolax* and *Onychocolax*, the plant body is monisiphonous, filamentous and entirely within the host, the fertile parts alone external to it. *Episporium* on the other hand is entirely external to the host except for the basal attachment processes. Even when, as occasionally happens, horizontal filaments are formed at a node, they lie between the free appendages of the nodal ring and the base of the succeeding internode. Consequently each pustule, or more rarely, small group of pustules, results from a separate infection, whereas in the other three genera a single infection results in an extensive internal thallus from which numbers of reproductive branches arise, in *Choreonema* in the form of small dome shaped conceptacles, in *Aiolocolax* and *Onychocolax* of small stalked branchlets. This striking difference in thallus construction is of course to a great extent conditioned by the structure of the host. The polysiphonous habit appears to be peculiarly suited to invasion by parasitic Florideae.

In the two last, both parasitic on polysiphonous algae possessing four pericentral siphons, there are certain well marked differences even in the internal plant body:—in *Aiolocolax* relatively simple, sparingly branched filaments growing parallel to the length of the host and producing fertile branches more or less in succession between pericentral siphons; in *Onychocolax* a much more lavishly branched system consisting of elongated filaments within each segment and a transversely spreading nodal plexus of shorter cells between successive segments. Resulting from these internal differences are marked differences in the occurrence of the fertile axes which emerge singly in the former, mainly in clusters at the nodes in the latter. Differences in the

external fertile axes are even more striking. An interesting feature peculiar to *Episporium* is the preponderance of bisexual pustules among the sexual branches in addition to the purely male pustules which also occur.

As regards the systematic position of the four algae, *Choreonema* is undoubtedly a member, if an aberrant one, of the Corallinaceae and has been thoroughly investigated, hence no more need be said about it here.

Of the remaining three, *Onychocolax* presents certain puzzling features, particularly the female axis, but the polysiphonous construction with four pericentral cells, whorled tetrahedrally divided tetrasporangia, four per segment, male organs, and the structure and development of the procarp and cystocarp all indicate affinities with the subfamily Lophothaliae among the Rhodomelaceae.

Episporium and *Aiolocolax* present greater difficulties. In *Episporium* thallus construction is unique; nevertheless the large central cell with cushion of small cells developed at its apex could be interpreted as comparable to thallus construction in Ceramium. The germination of the spore and struction of the naked cystocarp also suggest possible affinity with the Ceramiaceae. On the other hand in the construction of the cellular cushion itself, position and structure of the cruciate tetraspores and of the male organs it shows resemblances to the Cryptonemiales; the structure and position of the carpogonial branch, its behaviour after fertilization and the development of the carposporophyte appear to be most nearly related to some members of the Choreocolacaceae.

Of them all, *Aiolocolax* is perhaps the most puzzling. At first sight the four-celled carpogonial branch and the bearing cell with two lateral branches of one and two cells respectively appear to resemble a typical ceramialiam procarp, but the absence of a specialized auxiliary cell and development subsequent to fertilization are not characteristic of that order. Division of the apical cell though at first transverse later becomes oblique, and the cystocarp wall is unusual in its structure and mode of formation. The transverse division of the bearing cell subsequent to fertilization into a lower haploid and upper diploid portion could however be interpreted as a transitional stage leading to the type of auxiliary cell characteristic of the Ceramiales. Further, the wall of the cystocarp with its somewhat indefinitely two-layered construction and rudimentary pore could be similarly interpreted and *Aiolocolax* then be regarded as a primitive member of the Ceramiales. Nevertheless, it cannot be placed in any of the families at present recognized.

On the whole, therefore, for the present it seems best to regard both *Episporium* and *Aiolocolax* as genera of uncertain position, the former perhaps most nearly related to the Choreocolacaceae, the latter to the Ceramiales.

ACKNOWLEDGMENTS.

In conclusion I most gratefully acknowledge the inspiration and encouragement to work among marine algae which I owe to Dr. G. F. Papenfuss.

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EXPLANATION OF PLATES.

PLATE 1.

CHOREONEMA. EPISPORIUM.

- A, B. *Choreonema* on *Jania*. A $\times 32$, B $\times 78$.
- C-J. *Episporium centroceratis*. C. Very young pustule at node. $\times 285$.
- D. Slightly older female showing successive sheaths and developing trichogynes. $\times 285$.
- E. Heavily infected tip of branch of host; on the left a tetrasporangium of *Centroceras*. $\times 178$.
- F. Group of pustules; in the centre several young pustules, on the left a mature female with cystocarps. $\times 82.5$.
- G. A mature tetrasporic and H a mature male pustule with cushion slipped off the central cell, 'mace head' of latter seen in end view. $\times 82.5$.
- J. Two pustules, upper one with cystocarps, squashed to show central cells. $\times 82.5$.

PLATE 2.

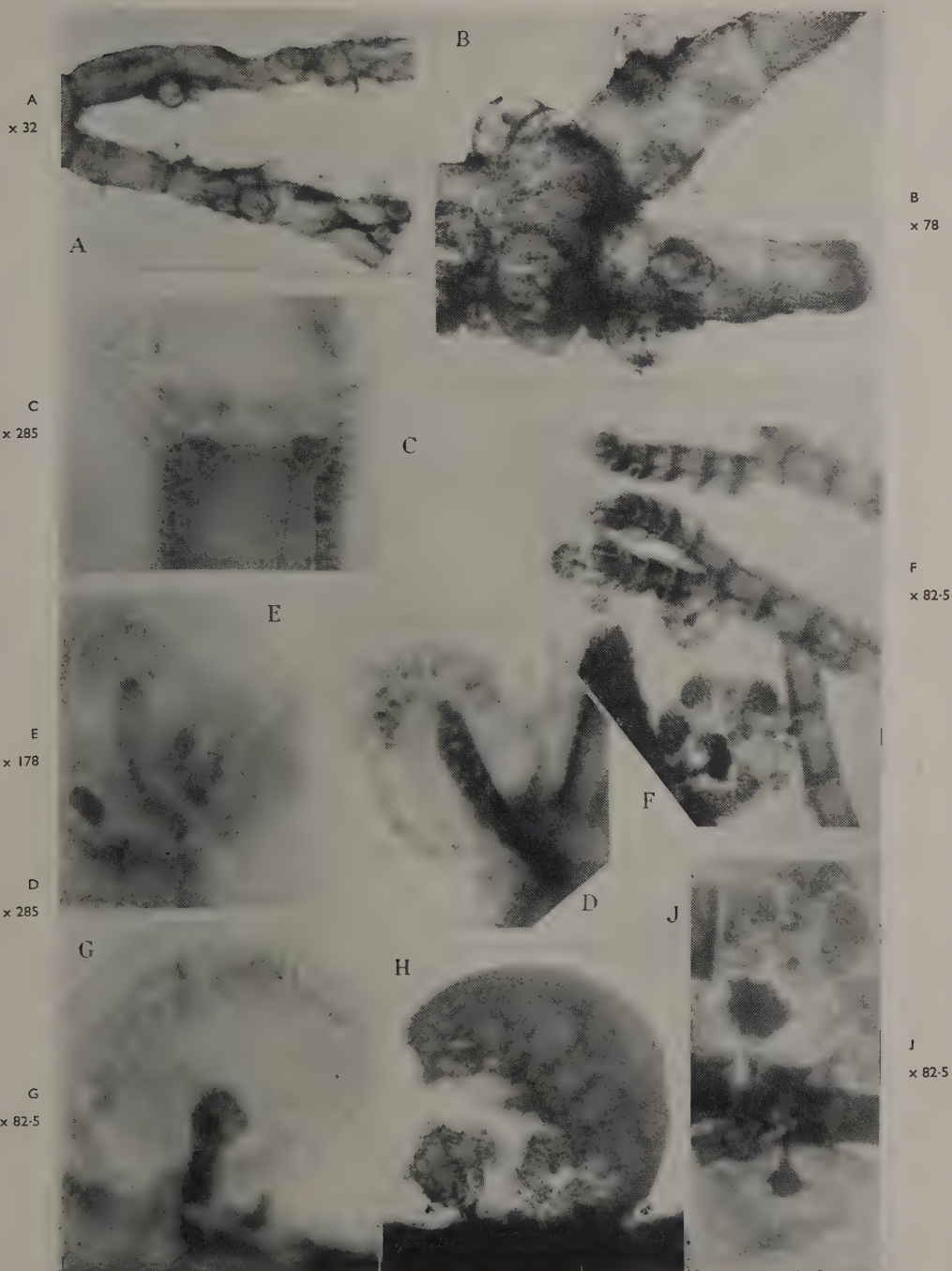
Aiolocolax pulchella.

- A. Branch of female plant of *Falkenbergiella caespitosa* with two young pustules of *Aiolocolax*, those on right showing young polysporangia. $\times 75$.
- B. Cystocarp of host with young fertile branch of parasite developing on it. $\times 150$.
- C. Young asexual and D older asexual pustules with polysporangia, in D majority already shed. $\times 120$.
- E. Top branchlet from D enlarged. $\times 350$.
- F. Three asexual branchlets stained to show structure; two on left seen in optical section, polysporangia shed from lower part, still developing above. $\times 170$.
- G. Two polysporangia, not quite mature, separated out from axis. $\times 360$.

PLATE 3.

Aiolocolax (contd.).

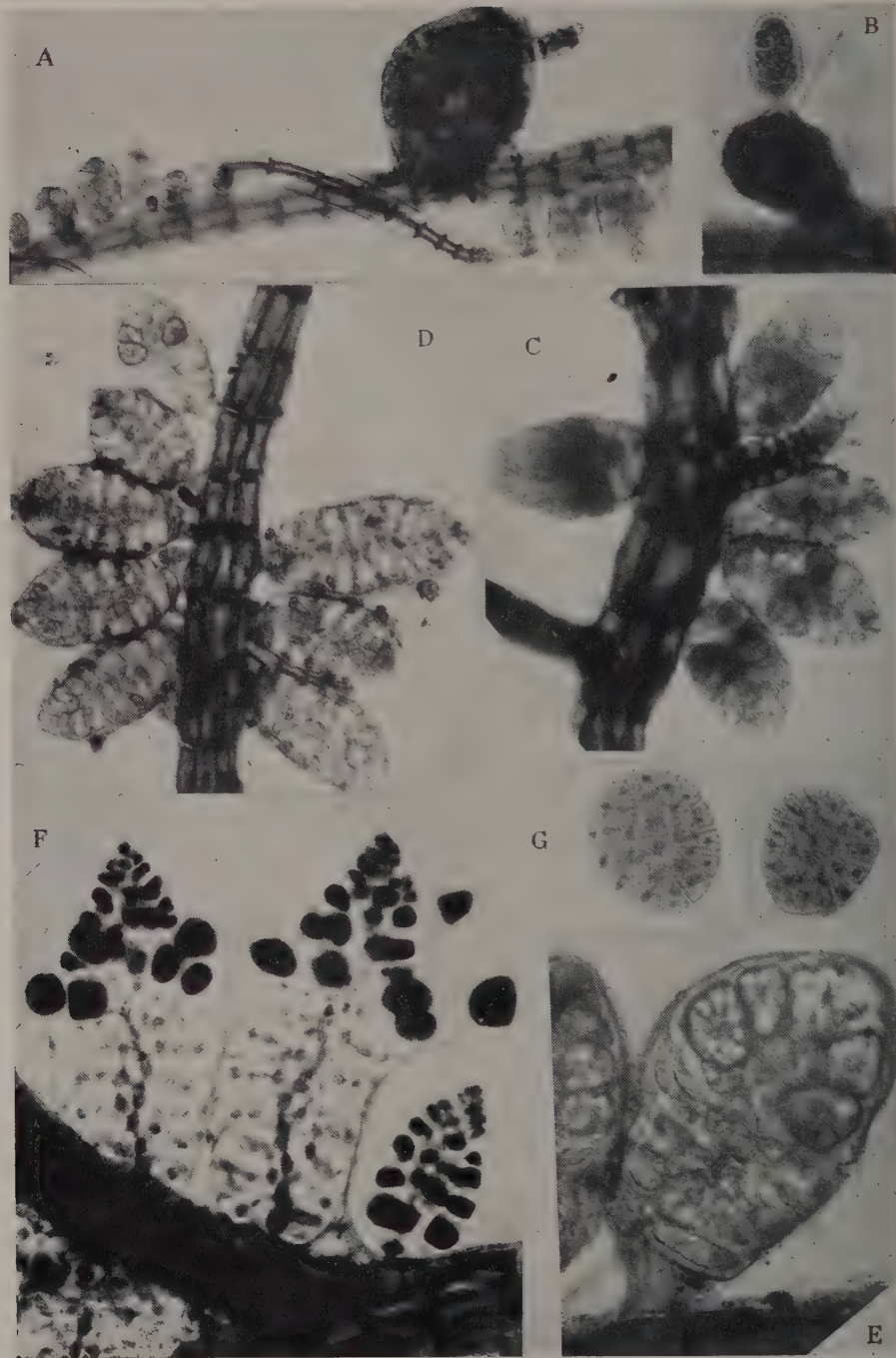
- A. Pustule showing five young axes, filamentous thallus visible in branch of host. $\times 350$.
- B. Mature pustules, male on the left (a very heavy infection), on the right female with developing cystocarps. $\times 75$.
- C. Exceptionally heavily infected branch with mature male axes, some hypertrophy in host. Partly squashed. $\times 75$.
- D. Mature male axis, showing filamentous thallus with stalk cell arising on it, escaping spermatia, central axis and apical cells still developing. $\times 360$.
- E. and F. Female pustules. E young showing trichogynes, F older with large developing cystocarps on left, on right five axes of varying ages, youngest below. Uppermost with cylindrical lower part, cystocarps developing near apex. $\times 75$.
- G. Female apparatus separated out (stained aceto-carmin) showing bearing cell with two sterile branches (one- and two-celled) and four-celled carpogonial branch above. Trichogyne broken off. $\times 550$.
- H. Carpogonial branch in situ, with long trichogyne; probably just before fertilization. $\times 550$.



CHOREONEMA

H
x 82.5

EPISPORIUM



A
x 75

B
x 150

D
x 120

C
x 120

F
x 170

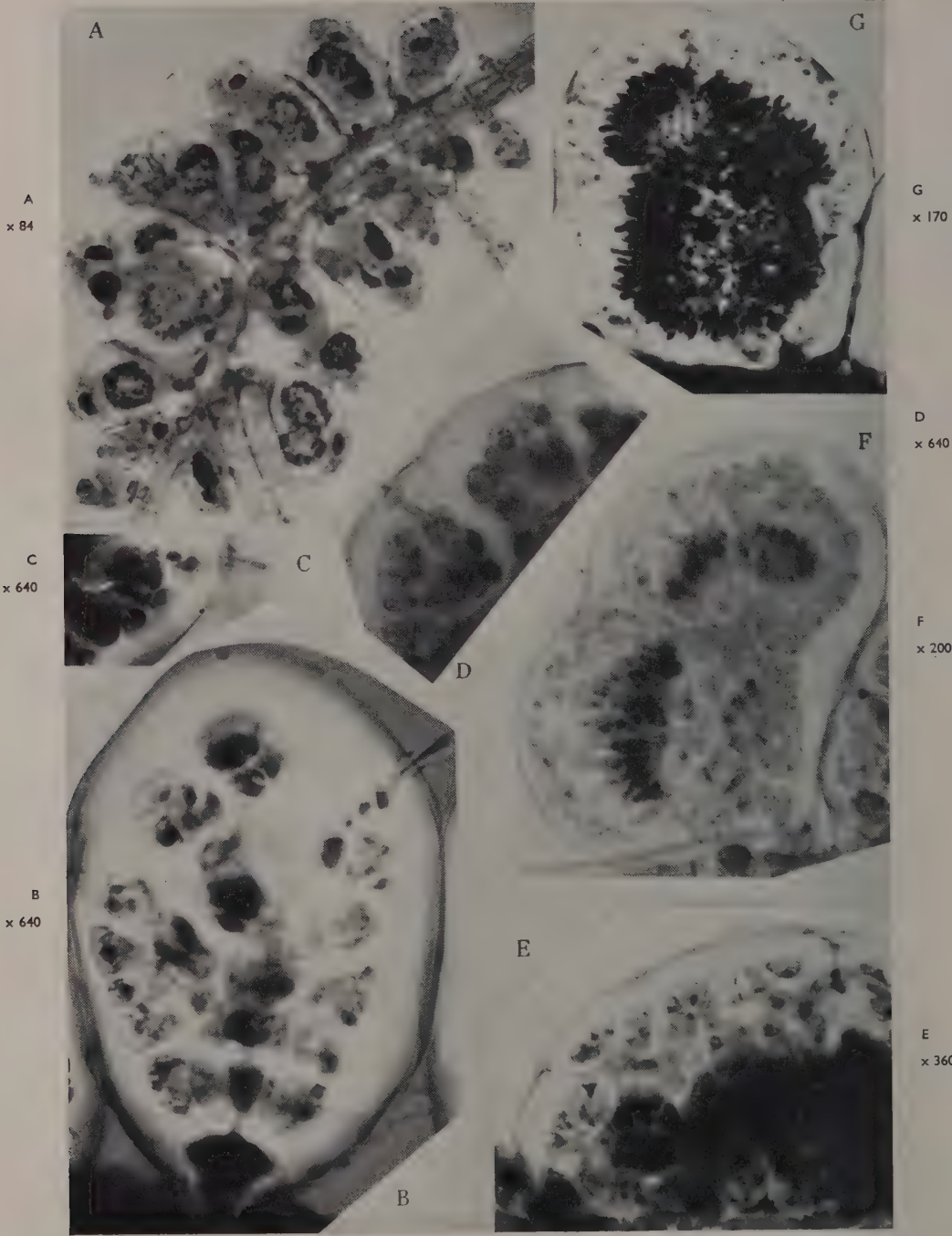
G
x 360

E
x 350

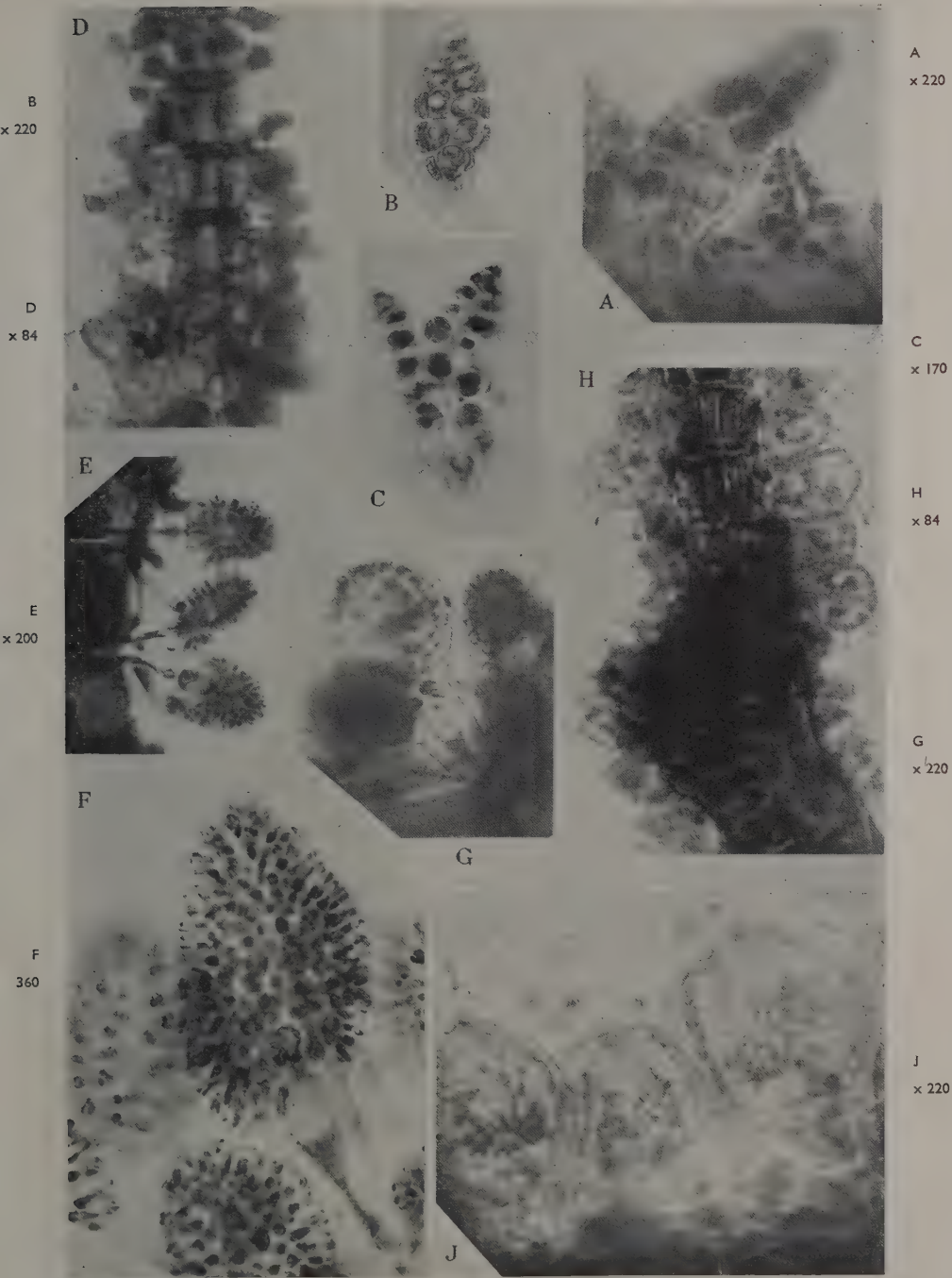


AIOLOCOLAX

H
x 550

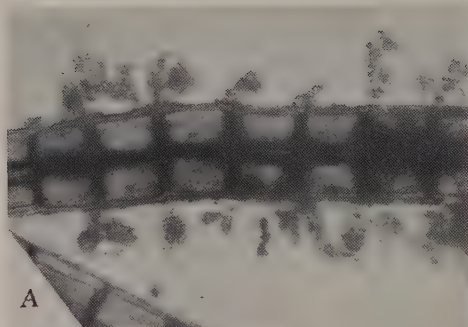


AILOCOLAX

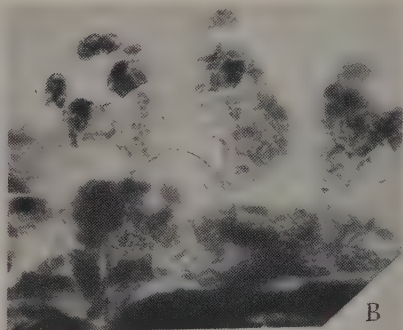


ONYCHOCOLAX

A
x 84



B
x 360

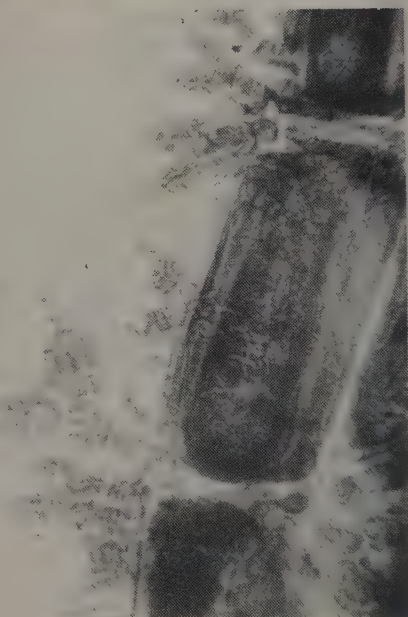


D

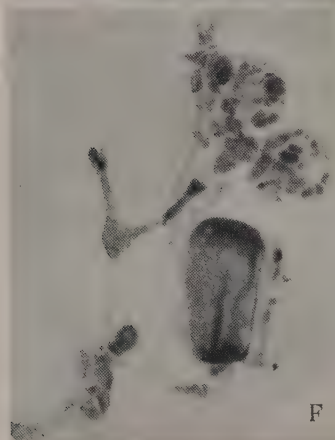
C
x 200



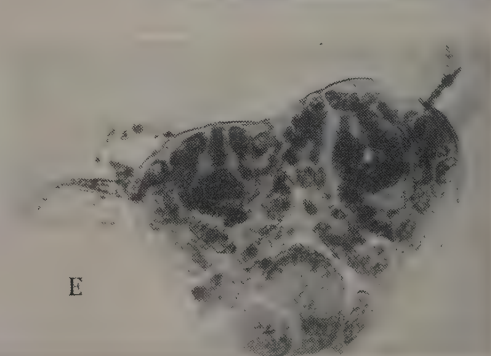
D
x 220



F
x 365



E
x 360



ONYCHOCOLAX

PLATE 4.

Aiolocolax (contd.).

- A. Particularly luxuriant female pustule stained with Fast Green to show developing cystocarps, several in each axis. $\times 84$.
- B. Young female axis in optical section showing stalk cell, axial cells with lateral branches and two developing carpogonial branches, the one on the left in the third segment hardly visible, that on the right in the fourth segment with trichogyne beginning to elongate, uppermost of the three small cells of the carpogonial branch lying in front of the base of the carpogonium. Envelope of the axis distended. $\times 640$.
- C. and D. Carpogonial branches in situ; C, a little older than B, uppermost small cell above the carpogonium, base of latter elongating downwards; D, showing relation of carpogonial branches (two) to one another and to the somatic cells of the respective branches. Slightly older than C, trichogyne broken away. $\times 640$.
- E.-G. Female axes with developing cystocarps. E, part of axis showing two young carposporophytes with remains of carpogonia above in space between developing branches of somatic cells. $\times 360$. F, older, with three cystocarps, a large one below and two small ones close together above. $\times 200$. G, still older with four developing cystocarps, remains of carpogonium still visible on right. $\times 170$.

PLATE 5.

Onychocolax polystiphoniae.

- A.-C. Tetrasporic. A, group of asexual axes in situ and B, a single axis (stichidium) separated out, both $\times 220$; C, a single stichidium branching above $\times 170$.
- D. Male pustule, older lower part causing hypertrophy of host; axes above still young. $\times 84$.
- E. Young male axes showing relation to host. $\times 200$.
- F. Mature males showing abstriction of spermatangia; on the left surface view showing groups of spermatangia, some three, some two in each group. $\times 360$.
- G. Two f axes, one with two cystocarps developing, one with a single cystocarp. $\times 220$.
- H. Female pustule, very heavily infected; below, axes still young, above, cystocarps mature; many carpospores scattered about. $\times 84$.
- J. Upper part on right enlarged. $\times 220$.

PLATE 6.

Onychocolax (contd.).

- A. Young female pustule, axes emerging at joints, showing claws and trichogynes. $\times 84$.
- B. and C. Young female pustules stained to show claws and developing fertile segments. B, still very young. $\times 360$; C, older, some with trichogynes showing, claws more pointed. $\times 200$.
- D. Female pustule showing relation to host and filaments between segments; two groups emerging between segments, small axis in centre internodal. Group on right still immature, large axis on left ready for fertilization, one trichogyne just visible $\times 220$.
- E. Female axis separated from pustule with two young cystocarps; in the one on the left three cells of the axis clear, the fertile axial cell shaped like a conical flask, with large nucleus, bearing cell visible below carposporophyte; origin of wall partly from first and third segments clear; in the one on the right, ostiole distinct. Below, the large basal cell with two pericentral cells visible, on the left a large one, on the right, smaller. $\times 360$.
- F. Female axis separated out from host with part of the filamentous thallus; a single pericentral cell of host on right. Abnormal, with three branches and three developing cystocarps. Branch on left showed two successive fertile segments. $\times 365$.

A STATISTICAL APPROACH TO THE PROBLEM OF THE PHYLOGENY OF A GENUS OF FERNS

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(With 7 tables.)

This paper consists of two parts. In the first is described a statistical technique which enables phylogenetic hypotheses to be put forward with an objectivity that has hitherto been difficult to attain. In the second, this technique is applied to the results of a morphological analysis of 71 species of *Elaphoglossum*, a genus of tropical ferns. It is shown that it is most unlikely

that the situation revealed by the analysis could have occurred by chance and a biological explanation must therefore be sought. Of the three possible explanations, that concerning the evolution of the characters considered is the most satisfactory.

I. THE STATISTICAL TECHNIQUE.

The method of analysis.

The principle underlying the technique to be described is that of studying the variation of two or more characters common to a group of allied forms simultaneously. It can best be illustrated by considering a general example.

Suppose all the species of a genus to show a number of basic characters, such as the presence of a vascular system of definite pattern, the possession of epidermal appendages of constant form and so on. These characters, it should be noted, are not those which are present or absent; they are common to all the species of the genus being considered. Further, suppose each character to show a range of expression in the genus, but the expression to be constant in the mature form of each species, and, within the genus, a connected expression, so that each character shows a well defined morphological series. This situation might be expected to exist in any genus which consists of a closely related series of genetic units. Further, suppose it to be possible to grade numerically the series in each character and to define each grade objectively, so that all observers will agree upon the state of the character in any given species.

TABLE I.

Analysis of a genus of 100 species in terms of the characters α , β and γ .

α_1	α_2	α_3
10	70	20
β_1	β_2	β_3
15	65	20
γ_1	γ_2	γ_3
20	70	10

Let, for convenience of example, there be two such basic characters in a given genus and let them be denoted by the symbols α and β ; further, suppose the morphological series in each character to be divisible into three definable and universally recognizable grades. The constitution of any given species in the genus in respect of these characters can then be denoted by a formula, for example, $\alpha_2\beta_3$, where the subscript figure denotes the grade of the character represented. Several species may, of course, have the same formula; they will differ in characters other than those which are being considered.

We can assume, as an hypothesis, that in any given species the grade which is displayed by one character will not have been influenced by the grades of other characters, that is, that the characters are independent and the grades are combined at random. The expectation of any particular combination is then dependent upon the relative frequencies in the genus of the grades of which it is composed. Thus, if the analysis of a genus consisting of 100 species has revealed that the frequencies of the grades are those shown in Table I, then the expected frequencies of the combinations of α and β are those shown in parentheses in Table II. The expected frequency of $\alpha_1\beta_1$ is $\frac{10}{100} \cdot \frac{15}{100} \cdot 100$, i.e. 1.5; the other frequencies are calculated in a similar manner.

If, however, the analysis of the genus has shown that the frequencies of the different combination are in fact those shown in bold type in Table II, there is clearly a considerable discrepancy from the expected values, especially in the top left hand cell, where $\alpha_1 \beta_1$ occur very much more frequently than would be expected. Such a discrepancy might be obtained by chance, but it is possible to estimate the probability of this happening, either exactly (Fisher, 1941) or less accurately, but adequately, by the calculation of the statistic χ^2 . The formula for this calculation is

$$\chi^2 = \sum \frac{((O-E)-0.5)^2}{E}$$

O =Observed value in each cell ; E =Expected value in each cell

The difference between the observed and the expected values in each cell is lessened by 0.5, a correction which makes for greater accuracy where small numbers are involved (Yates, 1934). The cells in which the difference between the expected and the observed values is less than 0.5 are neglected. The value of χ^2 for this example is 15.02. There are four degrees of freedom and the probability of obtaining such a value by chance is less than 0.01. The hypothesis that the grades of the characters are independent or combined at random is therefore unlikely. The cell $\alpha_1 \beta_1$ is particularly outstanding ; it contributes more than 60 per cent of the value of χ^2 . Were this a genuine example, the striking over-representation of $\alpha_1 \beta_1$ would demand a biological explanation.

TABLE II.

Comparison of the expected and the observed frequencies of the combinations of α and β in a genus of 100 species.

$\alpha_1 \beta_1$ 6 (1.5)	$\alpha_2 \beta_1$ 8 (10.5)	$\alpha_3 \beta_1$ 1 (3.0)
$\alpha_1 \beta_2$ 3 (6.5)	$\alpha_2 \beta_2$ 50 (45.5)	$\alpha_3 \beta_2$ 12 (13.0)
$\alpha_1 \beta_3$ 1 (2.0)	$\alpha_2 \beta_3$ 12 (14.0)	$\alpha_3 \beta_3$ 7 (4.0)

Note : The observed frequencies are in bold type, the expected, on the hypothesis of independence, in parentheses.

The advantage of using symbols for morphological characters and the objective numerical grading introduced here is that it enables an abstract treatment of the data free from prejudice and preconceptions, the twin dangers of all morphological argument. It also enables more than two characters to be considered simultaneously, without the confusion which results from pictorial methods such as those used by students of introgressive hybridization. In the example quoted above, it might be supposed that a third character, γ , also consisting of three grades, has been studied and found to be present with the frequencies shown in Table I. The expected frequencies of the twenty-seven different combinations can be calculated as before. It will be seen that there is again an outstanding discrepancy between the expected and the observed values in one corner of what will now be a three-dimensional table.

This table may be condensed to the form shown in Table III and the value of χ^2 calculated. This proves to be 35.84; there are four degrees of freedom and the probability of obtaining so high a value by chance is less than 0.001. Objection might legitimately be made to the use of the statistic χ^2 in this instance because of the very low expectation in the cell $\alpha_1\beta_1\gamma_1$. Nevertheless, the result obtained is meaningful since the effect of the introduction of γ into the analysis has been to increase the discrepancy between the expected and the observed values in the $\alpha_1\beta_1$'s, a portion of the table in which a marked deviation from expectation has already been revealed. Unfortunately, no exact treatment of a two by two by two table has yet been devised.

TABLE III.

Comparison of the expected and observed frequencies as in Table II, with the introduction of a third character, γ .

	$\alpha_1 \beta_1 \bar{\gamma}_1$ 0 (1.2)		$\bar{\alpha}_1 \beta_1 \bar{\gamma}_1$ 9 (10.8)
$\alpha_1 \beta_1 \gamma_1$ 4 (0.3)		$\bar{\alpha}_1 \beta_1 \gamma_1$ 1 (2.7)	
	$\alpha_1 \bar{\beta}_1 \bar{\gamma}_1$ 5 (6.8)	"	$\bar{\alpha}_1 \bar{\beta}_1 \bar{\gamma}_1$ 66 (61.2)
$\alpha_1 \bar{\beta}_1 \gamma_1$ 1 (1.7)		$\bar{\alpha}_1 \bar{\beta}_1 \gamma_1$ 14 (15.3)	

Note: $\bar{\alpha}_1$ signifies all the α 's which are not α_1 . Similarly $\bar{\beta}_1$ and $\bar{\gamma}_1$.

The combinations consisting of grades which are poorly represented in the genus have a very low expectation and this expectation falls sharply as more characters are considered. The inclusion of a large number of characters in the analysis consequently makes conspicuous the presence of these combinations of poorly represented grades.

The method of analysis described in the foregoing can be most satisfactorily applied to large genera consisting of closely related species. Since it is probable that not all the species of such a genus would be available for investigation, a point of practical importance is the choice of the material to be examined. If one or two samples of the species of the genus can be made and these can be regarded as random samples, the results will have meaning. If the distribution of the frequencies of the different combinations presents substantially the same picture in a second sample as in the first, and the samples have few species in common, then it can be assumed that real properties of the genus are being revealed and not artefacts due to the method of sampling.

The interpretation of the results.

If the analysis of a representative sample of a genus yields a result similar to that obtained in the imaginary example considered above, what biological explanation can be offered to account for the lack of independence between the characters? There are three possible explanations, concerned with the

developmental physiology of the species, the effect of natural selection and the phylogeny of the genus, respectively. The correct explanation for the particular genus under consideration must be determined in the light of evidence independent of the statistical analysis. The exact form of the explanation will also depend upon the particular circumstances relating to the genus, but the general nature of the three classes of explanation can be stated concisely.

(1). *Developmental physiology*. If the development of one character is physiologically linked, both in the embryo and subsequently with that of another or others, these characters are clearly never independent. Change in one character might inevitably lead to change in another, owing, for example, to a change in the distribution and availability of metabolites.

(2). *Natural selection*. It is conceivable that certain combinations of grades would possess a selective advantage over other combinations. In the course of evolution there would, therefore, be reason to expect the number of species possessing the favoured combinations to become greater than that of species lacking them. A statistical examination of the frequencies of the different combinations would show the selected combinations to be over-represented.

(3). *Phylogeny of the genus*. General biological experience suggests that the evolution of basic generic features, with which α , β and γ will inevitably be concerned, will result in morphological series, since a mutant must show a general structural relatedness to that from which it springs. The sense of these phylogenetic series may, of course, be different from that of the arbitrary enumeration of the morphological series adopted in the analysis, and the ancestral grade of each character may be at either extremity or even within these latter series.

It is legitimate to ask why these ancestral states of α , β and γ should persist in the genus. If they have never suffered from any selective disadvantage, there is no reason, other than accident or catastrophe, why they, or the combination of ancestral grades, should have disappeared in evolution. In these conditions, it can be assumed that the combination of α , β and γ possessed by the ancestors of the genus will still be found in it at a later period, although, of course, most probably in species morphologically different from the ancestral ones in characters other than those being considered. It will be shown in the second part of this paper that at least one genus exists in which there is reason to believe that these conditions are fulfilled.

It inevitably follows from the fact that a genus has evolved from ancestors possessing a certain combination of grades, and that this combination has persisted in subsequent speciation, that the distribution of the grades with respect to each other either in the genus or in a representative sample of it can never be at random. The combination of the ancestral grades of the characters will be represented more frequently than it would have been had the genus been created *de novo* and the grades of the characters combined at random. The statistical picture will resemble that in the imaginary example quoted.

The concentration of the ancestral grades in one part of the distribution will cause the chances of the most recent grade in each character being combined with the ancestral grades of other characters to be diminished. The most advanced grades in each series will, consequently, also tend to occur more frequently together than would be expected on the hypothesis of independence. The distribution of the frequencies of the different combinations is therefore polarized, the combinations of the ancestral grades and the most recent grades of each character occurring more frequently than would be expected on the hypothesis of independence. It should be noted here that, if the frequencies of the different combinations are distributed in this way and a phylogenetic explanation is to be invoked, there is no means of distinguishing

the combination of the ancestral grades from that of the most recent except by the introduction of evidence independent of and external to the statistical analysis.

It is now possible to proceed to an actual example, in which the statistical picture is similar to the imaginary one described above, and where, of the three possible classes of explanation, the phylogenetic appears to be the most satisfactory.

II. THE APPLICATION OF THE TECHNIQUE TO *Elaphoglossum*.

Elaphoglossum is a large genus of tropical ferns found principally in the humid forests of the mountains, many of the species being epiphytes. There are approximately 400 species and they display a closely connected range of form. Almost all possess an ovate-lanceolate frond and all possess Acrostichoid sori. The genus is of very uncertain affinities, although the fact that the few species it has been possible to examine so far have shown a basic haploid chromosome number of 41 (Manton and Sledge, 1954) suggests that it may belong to the Dryopterid alliance. The genus is widely distributed throughout the tropics, but about three quarters of the species are confined to the New World. Further progress in elucidating the affinities of the genus would be facilitated by knowing the evolutionary trends within it.

The available evidence suggests that *Elaphoglossum*, as a genus, is comparatively recent. It has no fossil history and, on a basis of comparative anatomy, it is an advanced form (Bower, 1928). There is reason to believe that much of the modern Polypodiaceous fern flora has evolved with the Angiospermous forest (Bell, in preparation) and the origin of *Elaphoglossum* may lie no further back than the Cretaceous period.

TABLE IV.
Grades of Stelar Symmetry.

	Grade
Dorsiventral two-ranked condition with bud traces posterior to each leaf trace (e.g. Bell, 1950, Fig. 3)	α_1
Dorsiventral three- or multi-ranked condition with bud traces associated only with the marginal leaf traces (e.g. Bell, 1950, Figs. 4 and 5)	α_2
Dorsiventral three- or multi-ranked condition with bud traces associated with the marginal and most or all of the dorsal leaf traces (e.g. Bell, 1955, Fig. 2)	α_3
Radially symmetrical condition with bud traces associated with most or all of the leaf traces irrespective of position (e.g. Bell, 1950, Figs. 6 and 7)	α_4

It will be seen, then, that *Elaphoglossum* possesses two features which make it a particularly promising field for scientific enquiry, namely, it possesses a closely connected range of species and it seems very likely that it has been in continuous evolution since the end of the Mesozoic. The tropical region has known little climatic change since the Cretaceous period (Axelrod, 1952; Brooks, 1926), so it appears likely that *Elaphoglossum* has not had to endure in its evolution those climatic vicissitudes which have been inflicted on temperate floras.

The morphological analysis of *Elaphoglossum* has been described in detail elsewhere (Bell, 1950; 1951 a; 1951 b; 1955). It will suffice to say here that three characters capable of grading exist in the genus, concerned respectively with the symmetry of the stele, the structure of the base of the petiole and the form of the scales of the lamina. These three characters are referred to in the order given as α , β and γ . The definitions of the grades are given in Tables IV, V, and VI and it will be seen that the grading is quite

objective. The analysis has been based upon two samples, the first of twenty-five species from Jamaica and the second of forty-six from Ecuador and reasons have been given (Bell, 1955) for regarding these as random samples of the species of the genus. The results of the analysis are set out in Table VII. It should be noticed that, since the total representation of α_3 and α_4 is so low in each sample, these classes have been combined in calculating the expected frequencies and in the subsequent statistical test.

TABLE V.

Grades of Development of the Petiolar Joint and Aerenchyma.

	Grade
Petiole without joint. Aerenchyma forming marginal ridges, obscure, rarely conspicuous (Bell 665), and soon dying out (e.g. Bell, 1955, Fig. 4, C)	β_1
Petiole jointed, but joint not sharply localized and not, or only a little, prominent. Associated colour change diffuse. Aerenchyma forming narrow marginal ridges, sometimes crenulate, but always <1 mm. high, dying out before the joint or ascending as faint marginal stripes (e.g. Bell, 1955, Fig. 4, B)	β_2
Joint well defined, localized, and usually prominent, associated with a sharp colour change. Aerenchyma in the form of pegs or flanges > 1 mm. high and confined to the base of the petiole near its insertion (e.g. Bell, 1955, Fig. 4, A), rarely absent (<i>E. nematorhizon</i> , <i>E. procurrens</i> , and Bell 346)	β_3

TABLE VI.

Grades of Development of the Scales of the Lamina of the Frond.

	Grade
Simple glandular hairs	} γ_1
Branched glandular hairs	
Capitate glandular emergences	
Laminate scales with basal attachment	γ_2
Laminate scales with cordate or lobed bases and the attachment at the base of the sinus	} γ_3
Laminate scales standing away from the surface, the base tending to be cochleariform, but the margins revolute in part only	
Bristle scales (e.g. as in <i>E. villosum</i>)	
Peltate scales (e.g. as in <i>E. tectum</i>)	γ_4

Note: The reasons for adopting this classification will be found in Bell, 1955.

Two points emerge from the data which are of immediate concern here.

1. The combination which is represented conspicuously more than expected in both samples on the hypothesis of independent combination is clearly $\alpha_1 \beta_3 \gamma_2$. This combination contributed approximately 23 per cent and 75 per cent of χ^2 in the Jamaican and Ecuadorean samples respectively. In the Jamaican sample the combination $\alpha_4 \beta_1 \gamma_4$ is also outstanding and contributes approximately 72 per cent of χ^2 . All other contributions to χ^2 are individually less than 7 per cent of its value in both samples.

2. There is a striking similarity between the distributions of the frequencies of the different combinations in the two samples, although they have only two species in common and were gathered from regions some 1200 miles apart. It is true that in the Ecuadorean sample $\alpha_4 \beta_1 \gamma_4$ occurs only once, but it will be noticed that, as in the Jamaican sample, β_1 is the only grade of β with which α_4 and γ_4 are together combined. The species with this combination is not one of those common to the two samples.

The interpretation of the analysis.

A biological explanation must be sought for the conspicuous over-representation of the combination $\alpha_1 \beta_3 \gamma_2$ in the Jamaican and Ecuadorean samples of the genus. It has been argued at length elsewhere (Bell, 1956) that there is no evidence to suggest that the characters α , β and γ are intimately connected developmentally. Nor is there any evidence in the field to suggest that the combination $\alpha_1 \beta_3 \gamma_2$ possesses any selective advantage, connected either with ecological factors or with reproductive or metabolic efficiency, which would cause it to be over-represented. In these circumstances the search for another explanation is fully justified.

As has been stated earlier, a satisfactory phylogenetic hypothesis requires independent external evidence to complement the statistical findings. In *Elaphoglossum* this evidence comes from the striking difference in the geographical distributions of the first and fourth grades of α . Whereas α_1 is generally distributed throughout the tropics, α_4 is, so far as is known, confined to the New World and is commoner there in areas which have been colonised by plants since Tertiary times. The most reasonable explanation of this disparity is that α_1 is the grade of greatest antiquity and that α_4 is comparatively recent in its appearance and has not yet become widely distributed. Of the intermediate grades, α_2 and α_3 occur in both hemispheres, but α_2 is less common in the Old World than the New and α_3 is distinctly rare in the Old World, being confined, so far as is known, to areas subject to recent volcanic disturbance and where, consequently, evolution may have been accelerated by the creation of new habitats. This evidence points to the series $\alpha_1 \rightarrow \alpha_2 \rightarrow \alpha_3 \rightarrow \alpha_4$ being in fact a phylogenetic series.

In the light of the theoretical considerations given in the first part of this paper, the over-representation of the $\alpha_1 \beta_3 \gamma_2$ now acquires considerable significance. This combination fulfils all the requirements given there for one consisting of ancestral grades, and there is independent evidence pointing to the antiquity of α_1 .

It should also be noticed that the combination $\alpha_4 \beta_1 \gamma_4$ fulfils all the requirements for one consisting wholly of the most recent grades. It is over-represented, conspicuously so in the Jamaican sample, and there is independent evidence for the recentness of α_4 . That it is in the Jamaican sample that the over-representation of $\alpha_4 \beta_1 \gamma_4$ is more conspicuous than that of $\alpha_1 \beta_3 \gamma_2$ is additional evidence in favour of the recentness of the former combination. There is geological evidence that Jamaica was submerged in the Oligocene and re-emerged in the Miocene, during part of which period there was a land bridge connecting the island with Honduras and Nicaragua (Schuchert, 1935). Whether the *Elaphoglossa* recolonising the island reached it along this land bridge or by aerial transport of the spores, they were inevitably representative of an *Elaphoglossum* flora that was no longer wholly primitive. The situation is different from that obtaining on the mainland, where a tropical mountain forest has probably been in existence since Cretaceous times, covering first the older Mesozoic mountains of the Guiana shield and spreading to the neighbouring Andes as these were uplifted in the Tertiary and where mountain building has continued to the present day. The fact that the Jamaican *Elaphoglossum* flora has evolved from ancestors that were not wholly primitive would result in a poorer representation there of the ancestral combination than in the Andes. This expectation coincides with the actual findings.

In the light of the evidence which has been assembled in the foregoing, it is possible to put forward the hypothesis that the ancestral states of the characters α , β and γ are α_1 , β_3 and γ_2 , and the recent α_4 , β_1 and γ_4 . This hypothesis has been arrived at by objective processes, not by intuition, and its validity remains to be tested, like that of all hypotheses, by subsequent observations and discoveries. A fuller treatment of all the information

concerning *Elaphoglossum* has been published elsewhere (Bell, 1955 ; 1956). What has been done here is to describe a technique which enables morphology to rank as an inductive science and which enables reasoned hypotheses to be advanced concerning the phylogeny of groups of related organisms of which we have no fossil record. There is no reason why it should not have wider applications.

The statistical method which has been used in this investigation is a modification and development of that introduced by Frost (1930 a, 1930 b, 1931) and Kribs (1934-5) and used in a limited form by Sporne (1948). The work described in the foregoing has caused the author to consider very carefully the conditions in which statistical findings can have valid phylogenetic significance. A failure to realise that these conditions are in fact very limited and that it is essential to show in each investigation of this kind that there is good reason to believe that they are satisfied is, in the author's opinion, a serious weakness of previous work in this field.

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GENETIC STABILITY IN POPULATIONS OF THE POLYMORPHIC SNAIL, *CEPAEA NEMORALIS* (L.)

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(With 6 text-figures.)

INTRODUCTION.

A number of collections of the polymorphic land-snail *Cepaea* (*Helix*) *nemoralis* (L.) made by the late Mr. H. H. Brindley at the beginning of the century are preserved in the University Museum of Zoology at Cambridge. Some of the collections are from very restricted and carefully defined localities and it has been possible to revisit the original sites to take further collections from exactly the same areas 40 to 50 years later and so to study the changes that have taken place in the genetical structure of these populations under natural conditions over a comparatively long period of time.

C. nemoralis is well suited to such studies since it occurs in a large number of easily recognized varieties, many of which are known or believed to be genetically determined. It is often found in small isolated or semi-isolated colonies differing markedly from each other in the proportions of different genes present, and these have been considered to be good examples of the "Sewall Wright Effect", the different populations drifting apart genetically as a result of the random assortment of non-adaptive genes. This view has, however, recently been strongly criticized by Cain & Sheppard (1950, 1954) who have proved conclusively that at least some of the genetic differences between different populations are due to the effects of visual selection by birds and other predators for the different shell patterns and colours against different backgrounds of vegetation. It is therefore of interest to be able to re-investigate a natural population after a long interval, especially where exactly the same area can be sampled and any changes in the environment assessed. It is important that the exact area covered by the original collection should be identified since with such a slow-moving animal the area in which completely panmictic breeding can be assumed to occur is extremely restricted and important differences in the genetic structure of different sections of the same continuous population may be found over distances of 100 yards or less.

One previous investigation of this kind in *C. nemoralis* has been reported briefly by Boettger (1931) who found striking changes after 15 years in a population near Frankfurt a/M. A collection of 223 shells made in 1924 'in a small area' which seems to have been among vegetable gardens, compared with 500 collected in the same area in 1909, showed an increase in the proportion of pink shells from nil to 43 per cent, of the single-banded 00300 variety from nil to 33 per cent, and a decrease in bandless 00000 shells from 64 per cent to nil and of the rare white lipped var. *albilabris* from 8.5 per cent to nil. Some changes had been made in the gardens since the first collection but hardly enough to account for these remarkable changes in the snail population, and Boettger suggests that the new varieties must have been introduced from elsewhere by man, presumably with garden plants. It seems likely that the original population must at some time have become greatly reduced or extinct to have allowed the newly introduced genes to have increased so much in such a short time, particularly as the gene for bandless shells, which decreased to nil, is known to be dominant to all the banded varieties.

Another investigation of a population of *C. nemoralis* over a period of three years has been reported by van Heurn (1943 and 1945) who found statistically significant changes in the proportions of different shell patterns and colours in collections taken from the same hedgerow from year to year. The largest change was in the five-banded shells which increased from 18 per cent to 32 per cent in one year, but in the following year these were down to 20 per cent again. Several other genes showed comparable fluctuations but there was no evidence of any constant directed trend.

Finally, there are the interesting observations that have been made on a colony of *C. nemoralis* artificially introduced into the United States at Lexington, Va., some 70 years ago (Howe 1898, McConnell 1935). The species is not indigenous in America but the snails have now spread over a considerable area and there were significant changes in the genetic make-up of the population after 32 years. This is, however, hardly to be compared with the present studies which are concerned with stable populations in very restricted areas.

VARIATION IN *Cepaea nemoralis*.

C. nemoralis is a highly polymorphic species and some 29 reasonably distinct varieties have been recognized by conchologists; the total number of named forms exceeds 200 (Taylor 1914). The principal shell colours are pink and yellow, which are allelomorphic with pink dominant, and brown, the genetics

of which is not known. The shell may have up to five bands running along the whorls and the bands are usually dark brown though in some forms they may be colourless, this being recessive to the normal colour. The bands may also be interrupted, smudged or occasionally split to give more than the basic number of five bands. Any one or more of the five bands may be absent and the completely bandless condition is dominant to all the banded forms. In the various banded classes as a general rule the lesser number of bands is dominant to the greater but the heredity of these forms has not been fully worked out. It is, however, known that the five-banded form is the universal recessive and is allelic with bandless, and that these are linked with the factors for yellow or pink shell colour, though there are different estimates of the degree of linkage (Fisher & Diver, 1934). Lastly, any two or more of the five bands may be fused together and, although the genetics of band fusion has not been investigated for *C. nemoralis*, in the sibling species *C. hortensis* (Müller) it is said that (12345) : (123)(45) : (12)3(45) : (12)345 : 12345 form an allelic series with the greater band fusion dominant to the lesser and showing no linkage with the five-banded-bandless locus (Boettger, 1950).

In the usual notation for describing the banding patterns the bands are numbered 1, 2, 3, 4 and 5 from the top of the whorl downwards, a band absent is shown as 0 and where bands are fused they are enclosed in brackets. Following Cain & Sheppard (1950) bands will not be counted as fused unless they are fused for at least 90° round the shell from the peristome, fusion occurring only near the lip being ignored. Some of the more important banding patterns and formulae are illustrated in fig. 1.

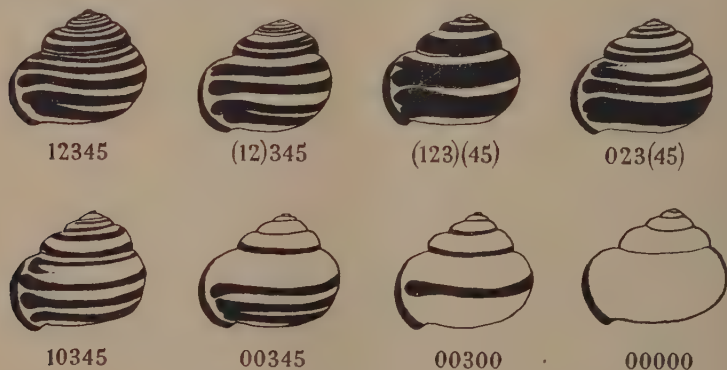


FIG. 1.—Banding patterns in *Cepaea nemoralis*. Natural Size.

MR. BRINDLEY'S COLLECTIONS.

It has been possible to make comparisons between three of Brindley's collections and samples taken from the same localities in the summer of 1953.

1. VEULETTES—CANY ROAD, NORTH FRANCE.

Brindley's original collection was labelled 'Veulettes—Cany road—1066 specimens from the first chalk pit from Pont Rouge and from east side of road 50 yards south—100 yards north of the pit. Aug. 13-14, 1906'. A recount in 1953 gave a total of 1115 shells in the box.

Veulettes is on the French coast 22 miles west of Dieppe and the road to Cany-Barville crosses the River Durdent by the Pont Rouge a quarter of a mile east of the village and then runs up the valley at the foot of chalk downs. There are two small abandoned chalk pits on the left-hand side of this road on

either side of a re-entrant into the downs some 500 yards south of Pont Rouge. The map reference of the northern of these two pits is 760406 on Sheet 19 of the 1/50,000 map of France, and there can be no doubt that this is the pit referred to by Brindley. The pit, which was visited in September 1953, is quite small with a chalk face about *30 feet high and 30 yards across, standing 15 yards back from the road. It has long been disused and the pit floor is now covered with a thicket of brambles and nettles with a few elder trees near the road, and with a small grass-covered talus at the foot of the chalk face. North of the pit the hillside comes steeply down to the road and is covered with rough but fairly uniform ungrazed grass with a few scattered bramble bushes. South of the pit the hillside runs away from the road up into a re-entrant leaving a narrow strip of rough grazing separated from the road by a ditch and grass bank. On the other side of the road over a bramble hedge and ditch there is a water meadow.

Collections of *Cepaea nemoralis* were taken from the area on 16th, 17th and 18th September in dull showery weather with plenty of snails out and active. Only eight living *Cepaea* were found in the chalk pit itself, all on the grass-covered talus, although *Helix aspersa* Müller was common. Two collections of dead thrush-eaten *Cepaea* shells were, however, taken from under clumps of elders and brambles on the pit floor. Some *Cepaea* were found on the roadside bank beside the pit, though they were not abundant there, but the population along the roadside petered out completely about 30 yards south of the pit. North of the pit the snails were much more abundant on the steep hillside as it ran down to the road for about 100 yards, after which there was a marked decrease in numbers though some snails were found up to 200 yards north of the pit beside the road. The snails were especially common within a few feet of the road, farther up the hillside they were much less easily found and the population would seem to be of the characteristic linear type often found beside roads (Lamotte, 1951). The other side of the road was also searched briefly but no *Cepaea* were seen.

The results of the collections are shown in Table I. Collection No. 1 was taken from a stretch of roadside extending from about 50 yards south of the centre of the pit to 50 yards north of it. Nos. 2 and 3 were collected on successive days from 100 yards north of the pit to 50 yards south of it, though only half a dozen more snails were found to the south. No. 4 was from the roadside between 100 and 150 yards north of the pit, No. 5 from the chalk pit itself and Nos. 6 and 7 are collections of empty thrush-eaten shells found under bushes from the south-west and north-west corners of the pit respectively. All the collections, except for No. 5, were taken from within about 10 feet of the road. Brindley's collection made in 1906 is included in the table for comparison and should be from exactly the same area as that covered by collections Nos. 1, 2, 3 and 5, 47 years later. No. 4 is possibly just outside Brindley's area if his measurements were accurate and taken from the centre of the pit.

Following Cain & Sheppard (1950) the banding patterns may be divided into two groups, 'effectively banded' where the first two bands 1 and 2 are present, and 'effectively unbanded' where they are absent. The reason for this classification is that from the point of view of visual predators it is the first two bands that are the most important since the others are largely hidden from view inside the whorls and underneath the shell in the living snail. The percentage 'effectively banded' for each collection is shown separately in the table, and also the percentage of shells that were pink in colour.

It is necessary first of all to consider whether the population in the area sampled is homogeneous in respect of the various shell patterns and this may be tested in a $2 \times n$ contingency table (Fisher, 1948) for the five samples of living

* 3 feet = 1 yard = 0.914 metres.

shells taken from the area in 1953. These tests indicate that the population is reasonably homogeneous along this 200 yards of roadside. There may be indications of a slight preponderance of banded shells near to the chalk pit but the 1953 collections are not large enough for a statistically significant demonstration that this is so. Any heterogeneity in the 1906 population cannot be estimated from the single sample available and so, for purposes of comparison, all the five samples taken from the same area in 1953 will be aggregated together.

TABLE I.

C. nemoralis collections from roadside south of Pont Rouge, near Veulettes, France.

Y = Yellow P = Pink	1906		1953 Roadside Collections Nos.						1953 Chalk Pit		
	Brindley		All Living						Living		Thrush-eaten
	Y	P	(1) Y P	(2) Y P	(3) Y P	(4) Y P			(5) Y P	(6) Y P	(7) Y P
12345	433	53	21	5	8	2	35	6	22	6	
(12)345		9		1				1			
1(23)45											
123(45)	37	4			1	1	2	2	1		
(12)3(45)	22	3	3		2		6	1	5		
(123)(45)	2	1	1							4	1
02345	26				1		1	1		1	
023(45)	1	1									
10345	41	2					2	1	2	1	1
00345	8	2									
00340										1	
00305	1										
00300	73	7	3	1	4	1	9	2	12	5	6
00000	355	34	28	1	25	3	57	2	42	1	18
TOTAL	1115		64	48	125	93			8	71	88
'Effectively Banded'	57%		48%	31%	44%	41%			50%	56%	68%
Pink	9.6%		10.9%	14.6%	9.6%	7.5%			12.5%	11.3%	11.4%

The results of such a comparison are shown graphically in fig. 2 from which it is clear that there has been a change in the proportion of 'effectively unbanded' shells from 43 per cent in 1906 to 58 per cent in 1953, which is highly significant ($P < 0.001$). This changeover is due almost entirely to an increase in the bandless 00000 gene at the expense of its recessive 12345 allelomorph amounting to about 12 per cent in the whole population over 47 years. Another 'effectively unbanded' pattern, 00300, has also increased by 2.3 per cent over the same period, which is proportionately about the same as the increase for 00000 though this is not statistically significant in the present samples, but the 00345 pattern, also classified as 'effectively unbanded', which formed about 1 per cent of the 1906 collection was not found in 1953. No new band formulae have appeared and all the other patterns, and also the total of shells with any bands fused, like the pink shell colour, have remained remarkable constant and show changes of only 1 or 2 per cent in the 47 years. The general picture of the 1906 population has been maintained with 12345 and 00000 shells predominating, all the other banding patterns forming only about 20 per cent of the total, and with about 10 per cent of the shells pink. The proportions of the different formulae found in this population correspond fairly closely to those found by Lamotte (1951) in a collection of over 100,000 shells from the whole of France, excepting that the preponderance of 12345 and 00000 was not quite so great in Lamotte's collections. However, in many natural populations, at least in England, these two formulae are not necessarily the

most abundant and 00345 or 00300 sometimes exceed the number of completely bandless shells while there is often a high proportion of fused bands among the banded shells.

The most likely explanation of the 15 per cent increase in effectively unbanded shells is that it is due to selection by birds (Cain & Sheppard, 1950) and there is good evidence from the two collections of broken shells taken from thrushes' anvils at the edge of the chalk pit that there is in fact selection against effectively banded shells in this population. The two samples of thrush-eaten shells, as shown in Table I, had 56 per cent and 68 per cent respectively of effectively banded shells. A 2×2 contingency test applying Yates's correction for continuity on the two collections gives $\chi^2=2.36$, which is not significant for heterogeneity so the two will be aggregated making a total of 159 thrush-eaten shells of which 63 per cent were effectively banded. This is significantly above the figure of 43.3 per cent for all five 1953 collections of living snails ($\chi^2=17.52$) and is also above the 48.6 per cent banded shells in collections Nos. 1 and 5 alone, the two taken from the immediate vicinity of the thrushes'

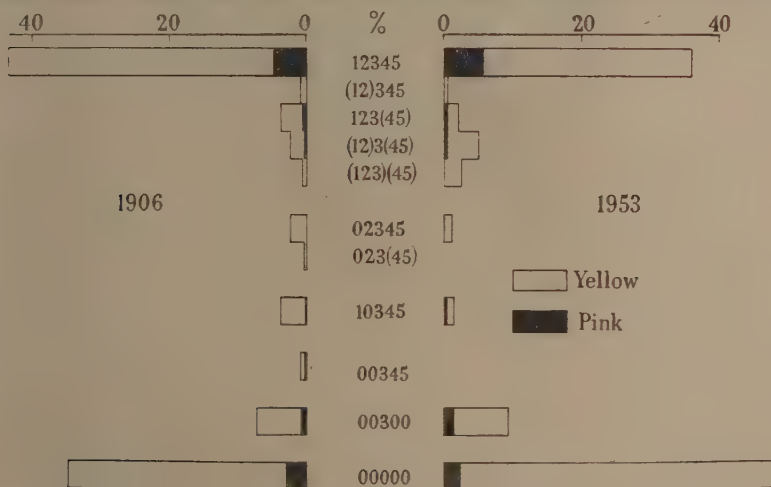


FIG. 2.—Composition of the *C. nemoralis* populations by the roadside south of Pont Rouge, near Veulettes, in 1906 and 1953.

anvils in the chalk-pit, though here the difference is just short of significance at the 5 per cent level ($\chi^2=3.60$). No anvils were found elsewhere in the area and as the stony ground under the bushes in the chalk-pit formed the most suitable anvil site, it is probable that the thrushes carried snails to it from the more abundant population farther up the road and that the predator selection against effectively banded shells was operating throughout the whole population. It is in fact to be expected that selection pressure should have been stronger away from the chalk-pit than in it where the background of rank vegetation and brambles might well have favoured banded shells. Sheppard (1951) has shown that there may be seasonal changes in selection pressure by thrushes correlated with changes in the vegetation. Most of the thrush-eaten shells found in this chalk pit in the middle of September would probably have been captured by the thrushes during the summer, when the vegetation was well grown and banded shells would be less conspicuous than on the barer ground of winter and spring, and so it is unlikely that the selection pressure of about 20 per cent against 'effectively banded' shells is an overestimate and it is rather remarkable that in the population as a whole

they should have decreased by only 15 per cent in 47 years. There is no reason to suppose that there have been any important changes in the environment over this period though the bushes in the abandoned chalk-pit may have grown bigger, but this is not likely to have increased the selection pressure against banded shells. The probable explanation would seem to be that there must be some other factor favouring the banded condition which partly balances the adverse effect of predation by birds, and Schnettér & Sedlmair (1953) have in fact recently shown that there are physiological differences between the different genotypes in *Cepaea*.

There is no evidence of selection by thrushes for shell colour (11·3 per cent pink in the thrush-eaten shells compared with 10·1 per cent in the aggregated five samples of living snails) nor for any of the intermediate banding patterns, all of which have remained extremely constant since 1906.

2. CHÂTEAU DE JANVILLE.

Brindley's collection is labelled 'H. nemoralis, Janville, South Ditch of Château. 436 adults. August 1906'. 448 shells were found in the box when they were counted in 1953, some of them not full grown.

TABLE II.
C. nemoralis collections from the Château de Janville.

Y = Yellow P = Pink	1906		1953		1953	
	Brindley		Château ditch		Beech Wood	
	Y	P	(1) Y P	(2) Y P	Y	P
12345	141	33	6	2	1	1
(12)345	3					
123(45)	19	8				
1(23)(45)	2					
(12)3(45)	12	2			2	
12045			2	1		
02345	31	7	1			
023(45)	4	7				
020(45)	1					
02300	1					
10345	13	2		1		
10300	1					
00345	14					
003(45)	1					
00340	2					
00300	57	12	6	4 1	1	4
00000	20	55	4 15	1 8	3	13
TOTAL	448		34	18	25	
'Effectively Banded'	64%		26%	22%	16%	
Pink	28%		44%	50%	72%	

Janville is a hamlet on the hill above Paluel two miles up the valley from Veulettes and there is a large 17th century château immediately to the south of it. At the end of a vista 100 yards wide and 200 yards long south of the château there is a sunken wall and ditch beside the road to St. Sylvain. The ditch is six feet deep and filled with rough vegetation and is separated from the road by a broad verge of scythed grass. There is open arable land south of the road but to the north and west of it are beechwoods through which the vista runs up to the château. There can be little doubt that this is the ditch described by Brindley and its map reference is 779384 on the 1/50,000 map.

The ditch was visited on 17th and 18th September 1953, and two samples of *Cepaea* were taken from it. The results together with Brindley's 1906 collection are shown in Table II. Both visits were made in wet weather very suitable

for hunting snails but few could be found. After nearly four hours' searching along the 100 yards of ditch and verge between the two woods, only 52 snails were found on the two days and these were all collected along about 20 yards of the road verge half way across the open vista. They included 12 recently dead intact shells, two of them with maggots feeding on the remains of the dead snails and two others that had been eaten by rodents.

There is no significant heterogeneity between the two samples for 'effectively banded' shells, for the pink shell colour or for any other character and they will be aggregated together for comparison with the 1906 collection from the same area, as is shown in fig. 3. It is obvious that a great change has taken place in this population during the past 47 years. Effectively unbanded

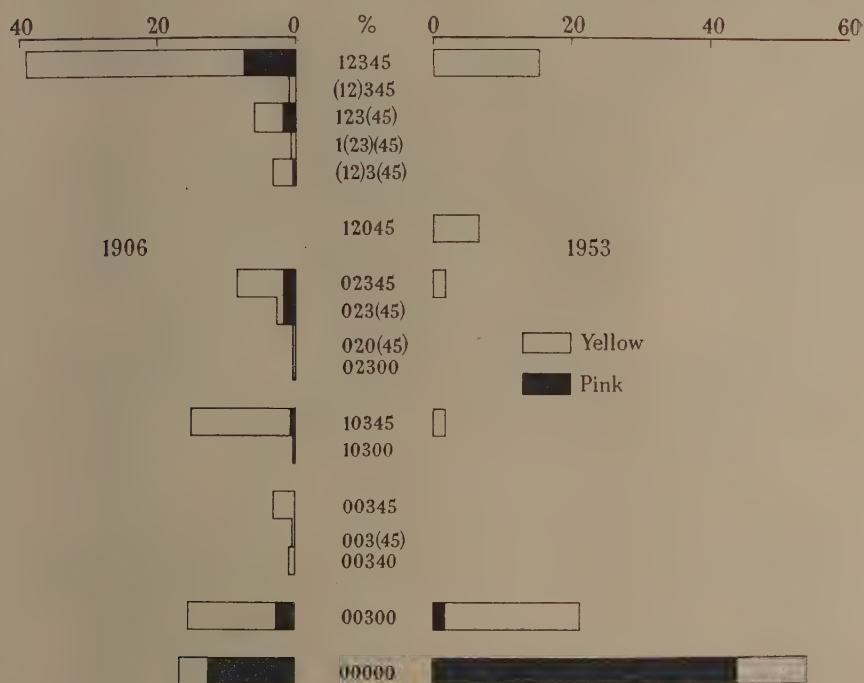


FIG. 3.—Composition of the *C. nemoralis* populations in the ditch of the Château de Janville in 1906 and 1953.

shells have increased from 36 per cent to 75 per cent, pink from 28 per cent to 46 per cent, while shells with fused bands, which formed 13 per cent of the 1906 collection (or 30 per cent of shells with two or more bands that could have been fused), were not found at all in 1953. The probabilities of these results being due to random sampling errors are of the order of 0.01 per cent or less. The other important change that must have occurred is in the total numbers of the colony, which must have been a large one in 1906 for Brindley to have collected nearly 500 snails from it probably in a single day, but which can scarcely have exceeded a hundred or so adult living *Cepaea* in 1953. It is unlikely that so large a change in the genetic structure of the population should have been brought about by selection by birds for the environment has probably changed little since the château was built and the vista through the woods must have been planned with the house. The colony in 1953 was

certainly small enough for genetical drift to have been important but it seems more likely that the 1906 colony has died out completely and that the present one has only recently been re-established. The small area occupied by it in 1953 and the fact that linkage between the pink and bandless genes has apparently not been broken suggests that this colony may have been derived from a single fertilized snail brought in from outside a few years previously. It will also be noticed that one of the few intermediate banding formulae in the 1953 samples is 12045, represented by three shells, and this pattern does not occur at all in Brindley's much larger collection, made in 1906.

The 1906 collection, with its preponderance of effectively banded and yellow shells is as would be expected from an open habitat of rough herbage, while the high proportion of pink and bandless shells found in 1953 is characteristic of beech woods (Cain & Sheppard, 1954). A small sample of dead but intact shells collected from the beech woods to the west of the château is included in Table II and it will be seen that it resembles the ditch collection in its proportions of both pink and effectively unbanded shells. The probable explanation therefore is that the small colony in the château ditch in 1953 had quite recently been established by a snail or snails probably brought in from the surrounding beechwoods and that it has no continuity with the large colony found there by Brindley in 1906, which has entirely disappeared. It would be interesting to see whether this new colony will eventually be brought by natural selection close in its genetical composition to the one that occupied the same area fifty years ago.

3. OTHER FRENCH COLLECTIONS.

Brindley's collections from this area include several other boxes of *C. nemoralis* labelled as from Veulettes, Paluel and the Château de St. Sylvain but the labelling was not sufficiently specific for the exact spots to be identified again in 1953 and no further samples were taken.

4. CAMBRIDGESHIRE COLLECTIONS.

Two other large collections of *C. nemoralis* made by Mr. Brindley have been traced, one of 276 shells said to have been collected in an area of 80 sq. yds. in a meadow near the River Cam at Waterbeach, Cambs., in 1892, but unfortunately the exact spot cannot now be identified, and the other of 467 shells from the wood on 'Crackling Hill' near Barrington, Cambs., collected in June 1911. This wood is almost certainly 'Hill Plantation' on Cracknow Hill (Ordnance Survey ref. 3750) a mile north-west of Barrington and six miles south-west of Cambridge. Other labels in Brindley's collection refer to 'Crackling Hill', Orwell, Cambs., and Cracknow Hill is in fact half way between Barrington and Orwell.

Cracknow Hill is formed by a ridge of boulder clay lying over the chalk, and 'Hill Plantation' is a small wood of 26 acres on the southern slope of the hill. Its greatest length from north-west to south-east is 550 yards and it is 250-300 yards wide. The upper end of the wood and most of the west side is a thick beech coppice, intermixed with elms towards the south, with bare ground beneath the trees, but there is a stand of ash in its north centre where the ground is covered with grass, wild strawberries and other vegetation. Most of the south centre of the wood has rather widely separated coppiced beech trees with brambles and rabbit grazed turf between them while the south end and south-east side consist of a dense hawthorn thicket with bare ground beneath the bushes. A hundred yards to the east of the main wood across a ploughed field there is a much smaller wood of 3 acres, 300 yards long and 50 yards wide, consisting of a hawthorn thicket at its southern end and with sparse beech trees in the centre and north. These two woods, illustrated

in fig. 4, were visited several times during August 1953 in wet weather and though few living *C. nemoralis* were seen, dead shells, both intact and eaten by birds and rabbits, were common on the ground. Samples of these were taken from ten separate areas in the larger wood, at the north-eastern (N.E.) and north-western (N.W.) ends in the beech wood, from the north centre (N.C.) in ash wood and from the open beech wood at the north-east centre (N.E.C.), from beech wood at the north-west (N.W.C.), south-west (S.W.C.) and south-east (S.E.C.) centre and edges of the wood, from brambles and open beech wood in the south centre (S.C.), and from beech wood with elms at the south-west (S.W.) and hawthorn thicket at the south-east (S.E.) ends. Three further collections were taken from the smaller wood, at the north end (N.) and centre (C.) among beeches and from the south end (S.) from hawthorn bushes. The areas collected are shown in the sketch map in fig. 4. A sample

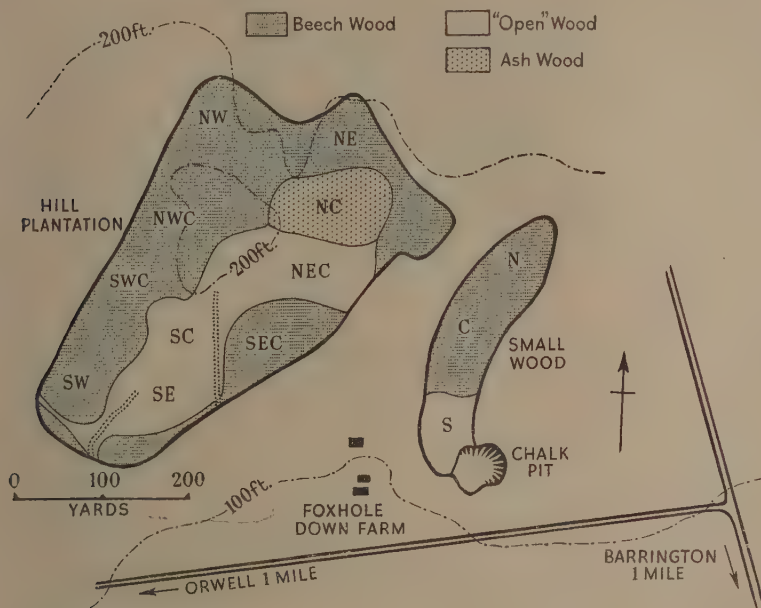


FIG. 4.—Sketch map of Cracknow Hill Plantation, near Barrington, Cambs.

of 100–150 shells was collected in each area, all shells seen being collected including a considerable number showing weathering that had probably been dead for a year or more. Shells were hard to find in the beech wood at the upper end (N.E. and N.W.) but elsewhere they were plentiful. The eaten shells included specimens broken open by birds and also by rabbits and possibly squirrels and rats, and though it is possible to identify the predator from the way in which the shell is broken (Morris, 1954), a significant proportion of the broken shells could not with confidence be assigned to any particular predator and the predators have not been classified separately.

The results of the collections with intact and eaten shells shown separately together with Brindley's 1911 collection are given in Table III, and fig. 5 shows the 1911 collection classified according to banding patterns and colour compared with the aggregated ten samples of intact shells from the larger wood collected in 1953. It is thought likely that Brindley's collection was taken

TABLE III.
C. nemoralis collections from Chacknow Hill Plantation.

from the larger and not the smaller of the two woods, but the two populations are very similar and the argument is little affected if they are taken together. The samples from the smaller wood are shown in Table III, but only the ten samples from the larger wood are included in the following calculations.

The first thing to be considered is the genetic heterogeneity of the population, shown by a comparison of the samples of intact shells taken from ten different areas of the wood, predated shells which may show the effects of selection being ignored. The figures for these samples are given in Table III and for each of the eight main characters studied (listed in Table IV) there is a significant departure from homogeneity ($P < 0.02$ per cent in each case) with a range of 20 to 30 per cent among the different samples. At the time that the collections were made in the different areas they were placed in one of two

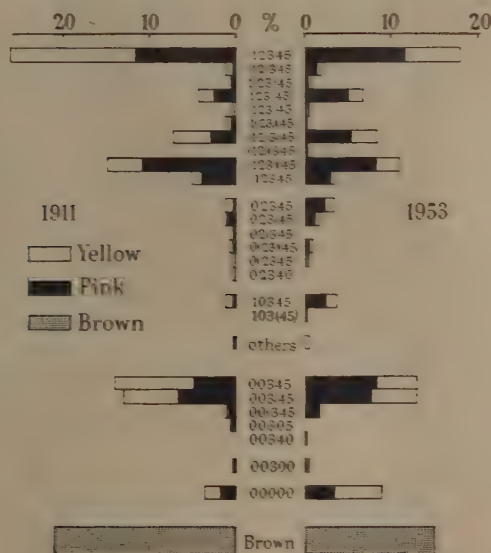


FIG. 5.—Composition of the *C. nemoralis* populations in Cracknow Hill Plantation in 1911 and 1953. The different banding formulae are shown as percentages of the total of yellow plus pink shells alone, excluding browns. The columns for brown shells show the percentages of browns above the total of pink and yellow, taken as 100.

categories, 'Beech Wood' where the beech trees formed a continuous canopy and with the ground beneath them bare of vegetation and covered with dead beech leaves, and 'Open Wood' where the beech trees, if present, were rather widely separated with the ground between them covered with vegetation, or with brambles and hawthorn bushes. In Table 4 the ten different areas have been grouped into these two categories, but it will be seen that the range of variability within the groups and the aggregate percentages for the different shell characters are similar, and χ^2 tests still show significant heterogeneity within each ecological group. Conversely, if the ten samples are arranged into two groups of high and low incidence of any particular character the grouping does not appear to have any ecological significance. So far as can be seen variations in the occurrence of different shell characters are quite irregular with the one exception of the 00000 pattern of no bands at all in pink and yellow shells, illustrated in fig. 6. This shows a fairly regular cline from 17 per cent of all pink and yellow shells at the southern end to few or none at its

northern end, which cannot be correlated with any obvious ecological change up the length of the wood. Dr. A. R. G. Owen, of the Department of Genetics at Cambridge, has kindly made a statistical analysis of the figures, from which it is clear that this regression is significant, notwithstanding the considerable local fluctuations. The situation, is however, complicated by the occurrence of brown shells, all of them unbanded, in the samples. Banded brown shells are usually extremely rare, though they have been found in some colonies (Cain & Sheppard, 1954), and at Cracknow Hill all the 387 brown shells collected in 1911 and 1953 were unbanded. The relationship between the dominant gene for bandlessness in pink and yellow shells and the bandless condition in browns is obscure, but there are indications that the same gene for bandlessness may be involved in both groups, and that it is closely linked with

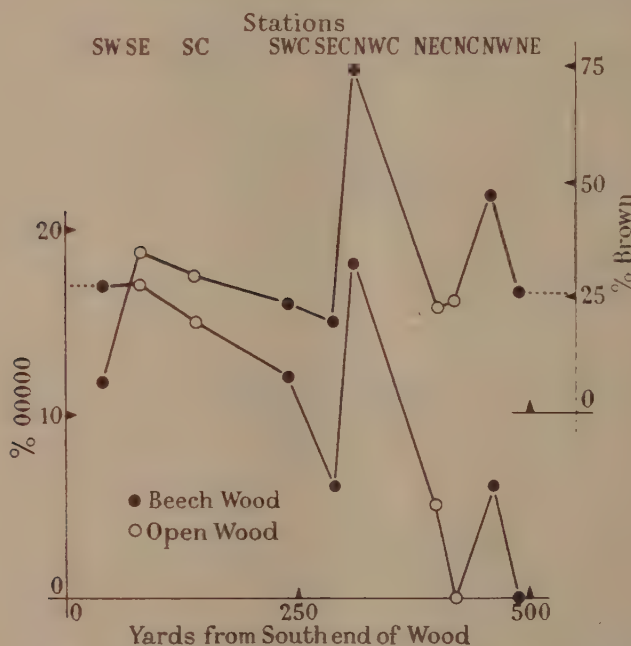


FIG. 6.—Percentages of bandless yellow and pink shells, and of browns, at different distances from the south end of Cracknow Hill Plantation. The percentages are of the totals of yellow and pink shells alone, excluding Browns.

the gene for brown which is not allelomorphous with that for pink and yellow. There must also be strong selection, probably physiological and effective at an early stage of development, against the crossing over of brown and banded. A line for the occurrence of brown shells (shown as the percentage above the total of pinks and yellows which is taken as 100) is also plotted on fig. 6 and it is interesting to see that this line appears to follow the fluctuations of the unbanded pinks and yellows, though it does not show any corresponding regular cline along the length of the wood. An analysis of the figures showed that, allowing for the regression in the bandless pinks and yellows, there does remain a residual correlation between the fluctuations of the two lines, although in the present samples the correlation is somewhat short of significance. If the effect is a real one it would be consistent with the hypothesis that the same gene for bandlessness is involved in both groups.

It is perhaps not surprising that no consistent distinction can be made between the *Cepaea* populations in the beech wood and that classified as 'open wood' since these two types of habitat are very much mixed up together in quite a small area. There can be few spots in the whole wood that are more than a hundred yards or so away from the other habitat type so that it is to be expected that immigration should swamp out any differentiation that might appear as a result of predator selection against the different backgrounds.

TABLE IV.—Percentage differences between the different shell characters found in the intact and eaten shells in the samples from various areas in the wood. Thus for the aggregated six samples from the beech wood stations 233 (52 per cent) out of 450 intact shells were 'effectively unbanded', compared with 100 (44 per cent) out of 226 eaten shells, so that the difference is shown as -8. In the 1911 column the difference shown is that between the percentage in the 1911 collection and the aggregated ten 1953 samples. Thus 53 per cent of the 1911 collection were 'effectively unbanded', and 52 per cent of the ten 1953 intact samples, so that the difference is shown as +1.

Predation Differentials	CRACKNOW HILL PLANTATION										Grand Totals 1953 1911			
	Beech Wood					Total	'Open Wood'					Total		
	NW	NE	NWC	SEC	SWC SW		NC	NEC	SC	SE				
Percent of whole sample	-6	-6	-7	+1	-5	-11	-8	-13	-3	-8	-20	-9	-8	+1
	+12	-4	-3	+25	-4	-5	+4	-9	-4	-8	-3	-5	+2	+7
	-14	-8	-2	-6	-3	+11	-4	+1	+2	-4	-18	-5	-4	+7
Percent of Pink and Yellowshells only excluding Brown	-4	-9	+7	-27	+22	+2	-5	+40	+2	-23	+10	+6	-1	-1
	+1	-2	+13	-10	+10	+15	+7	+8	+7	+3	+16	+8	+8	+9
	-1	-2	+2	+7	-10	+2	+2	+10	+9	+1	-2	+3	-1	-4
	+7	0	-6	+13	-4	-32	-7	-18	-1	-14	-15	-12	-9	-7
Percent of 000000	-	-	-4	-	+2	-4	-2	-	-	+8	+3	+3	+2	+2

* Including Fused Bands.

The whole wood should in fact be classified as a 'mixed deciduous wood' and the 27 per cent yellow and 52 per cent unbanded shells in the aggregated ten samples of *C. nemoralis* is typical of populations from mixed deciduous woods while none of the ten samples is near to the type characteristic of colonies in pure beech woods (Cain & Sheppard, 1954). It seems probable that the heterogeneity of the *Cepaea* population in this wood is quite irregular and that

the range of 20 to 30 per cent in the frequency of the commoner characters in different parts of the wood is within any limits that may be set by the effects of natural selection by visual predators in such a varied environment.

Since the *C. nemoralis* population in the wood is not homogeneous for any of the shell characters studied, a valid statistical comparison between the aggregated ten samples taken in 1953 and the single large sample collected by Brindley in 1911 from the wood as a whole cannot be made as could be done with the Veulettes and Janville collections. Nevertheless, it can be seen from fig. 5 and Table IV that the two collections are closely similar. For the eight shell characters listed in Table IV the difference between the 1911 collection and the aggregated 1953 samples is never as much as 10 per cent and in every instance the difference is well within the range of variation shown by the ten 1953 samples. Fig. 5 shows well the close resemblance of the two collections. Both have a high proportion of shells with fused bands giving an unusually large number of different banding formulae, and of the 29 different formulae found only eight do not appear in both collections, seven of them being represented by single shells and the eighth by a pair. In both collections bandless pink and yellow shells were uncommon and the single-banded 00300 form was rare, although in many other colonies 00300 is one of the commoner formulae. In both collections, apart from the bandless brown shells, the 00345 pattern, with or without its bands fused, was by far the commonest pattern in the 'effectively bandless' group, which is rather unusual. The Cracknow Hill colony is in fact rather distinctive in its genetical composition and it is probable that there has been little change in it over the period of 42 years; the collection taken from it in 1911 is in no way different from what might be expected to be found in a similar large sample collected from the whole wood at the present time.

Table IV shows the predator selection for or against the eight main shell pattern types in the ten different areas of the wood sampled. In the table the figure of -6 for selection in favour of 'effectively unbanded' at the north west corner of the wood means that the proportion of effectively unbanded shells in the predated sample was 6 per cent lower than in the sample of intact shells from the same area so that, if the difference is statistically significant, effectively unbanded shells are at a selective advantage compared to the others in this section of the wood.

There does seem to be consistent selection against effectively unbanded shells; in nine out of the ten areas sampled a higher proportion of effectively unbanded shells had been found and killed by predators than was present in the intact samples from the same areas, and in the one exception the difference was only 1 per cent. The mean rate of selection against effectively unbanded shells seems to be 8 to 9 per cent, which is statistically significant ($\chi^2=5.89$), and there is no difference between the beech wood and open wood type of habitat. Both the two main 'effectively unbanded' classes, 00345 and brown, show similar selective advantages in both open and beech wood and conversely 12345 is at a disadvantage in both habitats.

For the yellow shell colour there may be some selective difference between the two habitats, the mean disadvantage of yellow in the beech wood is 4 per cent, while in the open wood it seems to have a 5 per cent advantage. This is what would be expected since yellow shells will be more conspicuous against the predominantly brown background of beech woods, but actually the selection rates show considerable fluctuations within the two types of habitat and the difference between the two mean rates is only doubtfully significant. Band fusion possibly shows a similar effect, having a mean disadvantage of 6 per cent in the open wood habitats and an advantage of 5 per cent in the beech wood. This again is what would be expected since shells with bands fused show less of the ground colour and are generally darker so that they should be less conspicuous against the darker background of the beech wood.

Despite the apparent selection in favour of effectively unbanded shells there is hardly any difference between the 1911 and 1953 collections in the proportion of all unbanded shells; although brown shells have decreased by 7 per cent since 1911 this is balanced by an increase of 7 per cent in 00345. Since, however, the two populations that are being compared are not homogeneous in respect of either of these two characters the rather small changes in their proportions in the two collections have little significance.

Sheppard (1951) has shown that there may be important fluctuations in the selective advantage of different shell colours in visual predation, depending on seasonal changes in the amount of green vegetation in the environment. All the samples from Cracknow Hill were collected in the month of August, but many of the shells had probably been dead for some months before being collected and they probably include shells that had been selected by predators throughout most of the year. The rather wide variations in the apparent rates of selection for different shells characters in different parts of the wood may well be due to different samples having different proportions of shells selected by predators early and late in the season. However, the lack of evidence of any important change in the whole population of the wood over 42 years suggests that, whatever seasonal fluctuations in rates of selection there may be, on balance over a long period the population is in equilibrium.

DISCUSSION.

These three pairs of collections taken from the same localities after intervals of 40 years and more illustrate several interesting points.

The value of the comparisons that can be made between the pairs of collections from the two localities in France lies in the fact that it has been possible to identify exactly the very small areas from which Brindley's original collections were taken. With such a slow moving animal as a snail genetic heterogeneity in a population can be established over distances of the order of a hundred yards and rigorous comparisons cannot be made between samples taken indiscriminately from an area large enough to show any significant heterogeneity in its population. The colony in Cracknow Hill Plantation, which is quite a small wood, is certainly large enough for this effect to be shown, but at Veulettes the colony does seem to be homogeneous at present and there is no reason to suppose that it should have been any less homogeneous when the first collection was made in 1906.

The history of the *Cepaea* colony at Janville shows that it is quite possible for a numerous and flourishing population to become very restricted in numbers in the course of time and even to become extinct, and then subsequently to be re-established. It is therefore dangerous to argue that any particular population is so large that its genetic make-up can owe nothing to the random non-selective effects which, as has been shown by Sewall Wright (1940), can theoretically be of importance in populations restricted to a hundred or so breeding adults. A colony numbering thousands of individuals may in the quite recent past have been reduced to the few dozens needed for genetic drift to have occurred and natural selection will need some time to bring the population back into stable equilibrium with its environment. There is furthermore the possibility that in a species showing balanced polymorphism for a considerable number of genes, as is probably the case in *C. nemoralis*, several different combinations may be capable of establishing a satisfactory equilibrium in similar environments so that even where selection is of paramount importance the particular combination selected may owe much to the chance constitution of the original population upon which selection has been acting.

The increase of 10 to 15 per cent in the dominant gene for bandless shells in the Veulettes colony over 47 years can with confidence be ascribed to the selection exerted in its favour by bird predation. There is good evidence that

thrushes were selecting in favour of bandless shells in 1953 and the absence of any significant changes in the proportions of other shell characters makes it probable that the colony has maintained its numbers since 1906 above the level at which genetic drift could have been effective. This may be taken as confirmation of the suggestion made by Cain & Sheppard (1950) that shell banding patterns are of selective significance under natural conditions. It is indeed rather surprising that the bandless shells should not have increased more than they have done since Brindley's time, in view of the comparatively strong selection in their favour, and this suggests that the recessive allelomorph for the 12345 pattern may have some physiological advantage to balance its selective disadvantage in bird predation. If this is so, it means that a stable equilibrium cannot be achieved if predation rates are variable, as they probably are. It is worth noting that, however strong predator selection in favour of the 00000 phenotype may be, colonies consisting wholly of bandless shells are seldom if ever found in *C. nemoralis* (Lamotte, 1951) though the almost complete absence of the bandless gene is less uncommon.

In the Cracknow Hill colony the position is rather different as here there are a considerable number of genes involved in the polymorphism, many of them of considerable importance. So far as the evidence goes the population seems to be in equilibrium with its environment, though it is not possible to say whether this is due to seasonal differences in the rates of predator selection for the different shell patterns and colours, or to a balance between predator selection and differential viability of the various genotypes. The more abundant shell characters show similar ranges of variation of 10 to 15 per cent on either side of similar means in the samples from the two different habitat types found in the wood, and this suggests that within this range the genetic constitution of sections of the colony may vary independently of predator selection. It is also clear that the 'effectively unbanded' class can be made up of several different patterns in different proportions, all of them probably similar in selective value so far as visual predators are concerned but not necessarily of equal viability in competition with one another. The apparent cline up the wood shown by the bandless pink and yellow shells, which seems to be independent of any environmental change, may well be due to differential viability between this gene and others in the effectively unbanded class, rather than to predator selection. Unfortunately, no conclusions about the status of this cline in 1911 can be drawn from Brindley's collection.

The collections made in 1953 at Veulettes, Janville and Cracknow Hill are preserved in the Cambridge University Museum of Zoology, together with Brindley's collections from the same localities made in 1906 and 1911.

SUMMARY.

Collections of the polymorphic snail *Cepaea nemoralis* (L.) have been taken from three small and well-defined localities after intervals of 40 to 50 years.

In one of the areas the original colony has probably become extinct and it has recently been recolonized by a new population which is significantly different from the original one.

In the other two colonies the genetic composition of the populations has remained remarkably constant over the period covered by the observations, although in one of them there has been an increase of 10 to 15 per cent in the dominant gene for bandless shells. There is evidence that this change has been brought about by selective predation by birds.

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THE BROWN TROUT RESEARCH LABORATORY

By K. A. PYEFINCH.

INTRODUCTORY REMARKS.

The purpose of these remarks is to attempt, briefly, to sketch the history and development of the Brown Trout Research Laboratory and to link together, by providing a general picture of the laboratory's work, the individual contributions which follow.

The Brown Trout Research Laboratory was started, just over six years ago, in July 1948, jointly by the Scottish Home Department and the North of Scotland Hydro-Electric Board. Both these bodies had direct interests in research on brown trout. The Hydro-Electric Board's interest arose from the fact that their plans for hydro-electric developments would eventually place a large proportion of the freshwaters of the Highlands under their control and they were anxious to develop angling facilities on the impoundments and reservoirs they were to build. The Scottish Home Department (or their pre-war predecessor, the Fishery Board for Scotland) had long felt it desirable that their research work on salmon should be extended to other freshwater fish and they had, in fact, prepared a scheme of research on brown trout before the second World War. The economic conditions in the thirties had prevented this scheme starting but the improvement in the economic climate after the war, aided by the stimulus provided by the interests of the Hydro-Electric Board, resulted in the establishment of a small laboratory to carry out investigations into the biology of brown trout.

Pitlochry is situated roughly in the centre of Scotland and is reasonably accessible from the main towns and cities. The area round provides a wide variety of types of freshwater, both streams and lochs. Though Pitlochry was selected as the site for the laboratory largely because of its importance in the Tummel-Garry Hydro-Electric Scheme, there are, therefore, other reasons why this area is a suitable one for freshwater fisheries work.

It was fortunate that the terms of reference of this laboratory were wide. They can be briefly expressed as the investigation of the biology of brown trout with particular reference to the improvement of trout fisheries in Scotland. The broad basis of these terms of reference was fortunate in two ways. First, they enabled the laboratory to recruit, not only zoologists interested in fresh-

water fisheries but also the other specialists necessary for the full investigation of fisheries problems and second, they enabled fisheries problems to be studied on fundamental lines. This, it may be suggested, is especially important because it would seem that significant and permanent improvements in trout fisheries can only occur when the complex inter-actions of trout with its edaphic and biotic environment are understood fully enough for practical measures to be based on sound biology. In certain cases, of course, a decline in trout fisheries may be due to obvious causes such as gross pollution, but there are many more cases where the causes of changes are more subtle and less obvious and these, it may be suggested, are most likely to be discovered if we can first build up a useful body of fundamental knowledge.

In the course of the short symposium to be presented to you to-day, papers will be given which illustrate some of the work which is in progress in the chemical, botanical and zoological sections of the laboratory. In preparing their contributions to this symposium my colleagues have deliberately selected topics which they hope will be of interest rather than attempt to give summaries of the work done by their sections. The latter could only too easily result in a dull catalogue of what might appear to be routine activities whereas the former will show, it is hoped, some of the problems which are being faced.

The first two contributions, that by Mr. Holden and that by Dr. Brook, deal principally with problems associated with the major field project so far attempted by the laboratory, the possibility of effecting a significant improvement in a trout fishery by adding nutrients to the water. This is not the place to discuss the pros and cons of fertilization as a practical measure for improving a fishery but it is sufficient to say that our work on this topic (which is still in progress), though it has revealed many of the difficulties of this process, is also helping us to build up a clearer picture of the structure of the freshwater community in Highland waters. The third contribution, by Mr. T. A. Stuart, describes some of the results which are being obtained from what may broadly be termed investigations of the breeding biology of trout. There is a good deal of general information on the biology of trout but this work is showing that there is still much to be learnt which is not only significant fundamentally but which is also of considerable practical importance.

It should be added, however, that the three sections represented in this symposium today do not cover the activities of the laboratory completely as a good deal of work is also being, or has been, carried out on the bottom fauna and the zooplankton. It has not been possible to include accounts of the investigations on these parts of the freshwater community in this symposium to-day but they are making an important contribution to the general programme of the laboratory and any introduction to an account of the laboratory's work would be incomplete without mentioning them.

OBSERVATIONS ON THE ADDITION OF CHEMICAL NUTRIENTS TO SMALL LAKES

By A. V. HOLDEN.

Among the methods which the Brown Trout Research Laboratory is studying in attempts to improve the stock of trout in Scottish waters is that of using fertilizers to increase the quantity of available fish food. The fertilization of fish-ponds is a well-established procedure in many parts of the world, notably the tropics, but most of the knowledge obtained in Europe has been derived from experience with carp ponds. In such cases the increase in algal or macrophytic flora following fertilization is of direct benefit to the fish population. Salmonid fish, however, are not likely to respond quickly to fertilization owing to their carnivorous diet, and any improvement derived

from the process must come indirectly, from the development of a bottom fauna population which multiplies as the result of an increase in the algal flora on which it may feed. Nevertheless, some success has been achieved with artificial fertilizers in shallow trout rearing ponds in Germany.

A detailed study of the waters of several small hill lochs was made over a period of two years, involving regular analyses for pH, bicarbonate alkalinity, calcium, magnesium, nitrate and ammonia nitrogen, silica, and phosphate. From this study, a knowledge was obtained not only of the differences between lochs, but also of variations within a loch, and of the seasonal changes which might be expected to occur. In addition, some correlation could be attempted between the chemical data and that obtained for the flora and fauna generally.

The types of fertilizer which have been used by fish culturists are many, but the two constituents which feature most frequently are calcium and phosphorus. The presence of a high calcium concentration in water usually implies a pH on the alkaline side of neutrality, and a high bicarbonate concentration. This has been brought about by the solution of calcium carbonate (occurring as chalk or limestone) by the action of carbon dioxide, and waters of this type are usually good trout waters, if other biological factors governing the existence of trout are suitable. It is natural, then, that attempts should be made to improve poor, acid waters by treatment with ground limestone or chalk.

Phosphorus, probably the most important major nutrient in living organisms, is normally found in remarkably low concentrations in most natural fresh waters, and in Scottish waters the level of phosphate phosphorus is below the limit of detection, 0.5 μg . per litre. That in organic or particulate form, in plankton or suspended matter generally, is rarely above 20 μg . per litre, and frequently below 10 μg . per litre. Consequently the addition of even a few hundredweights of a phosphate fertilizer to a small loch can raise the soluble phosphate concentration some hundreds of times. Phosphatic fertilizers are in fact the most successful of all fertilizers which have been used by fish culturists.

There are two factors of fundamental importance in the application of fertilizers to small ponds or lakes, namely the frequency with which the water may change, and the action of the bottom deposit. To deal with the rate of turnover first, it is not unusual, in a small loch, for the quantity of water flowing through in a week to be as great or greater during a period of heavy rainfall, than the volume of the loch. Such a flow would result in a considerable loss of added soluble nutrients and lochs subject to frequent spates are obviously unsuitable for fertilization.

The second important factor, the bottom deposit, is a complex one. Basically, it may act as a reservoir for most nutrients, releasing them by ion-exchange, or removing them from the water by the same process. Bacteria and other micro-organisms in the mud are largely responsible for the breakdown of decaying organic matter to simple nutrient ions, many of which remain in the surface layers. The muds of slightly acid lochs in particular appear to have a considerable capacity for adsorbing nutrient ions added in the form of fertilizers, and this may be largely responsible for the rate at which certain nutrients, particularly phosphate, disappear. In deep lochs, the lower depths are almost devoid of oxygen for part of the year, and a release from the mud of adsorbed ions, such as phosphate, occurs. These nutrients are eventually made available to organisms in the surface layers as a result of the circulation of the water. However, the trout lochs which have been the subject of our study are relatively shallow, normally less than thirty feet in maximum depth, and never exhibit any oxygen deficiency, except under extreme conditions of prolonged ice cover. Under normal conditions, no detectable concentration of phosphate is ever observed in the surface waters. Although some release

of phosphate must occur as a result of the decomposition of organic material and exchange processes at the surface of the bottom deposit, that existing in free solution at any instant must be extremely small, and quickly utilized by the microflora and bacteria present.

The addition of a phosphatic fertilizer at the rate of one hundredweight per acre of loch surface produces an abnormally high concentration of phosphate ions in the water in a shallow loch, but this gradually decreases as the result of a combination of factors. In the summer of 1952, 40 cwt. of superphosphate was added to Loch Kinardochy, a 40-acre loch in Perthshire, with a mean depth of 8 feet. The initial concentration produced was about 330 μg . phosphate phosphorus per litre, and the decline was approximately exponential over the first 14 weeks i.e. the logarithm of the concentration decreased linearly with time. A dilution process alone could account for this decrease, but whereas this explanation would necessitate an average rate of outflow of about 4.5 cubic feet per second the actual average outflow over the period was nearer 0.5 cubic feet per second. Throughout the period, analyses were made of the total phosphorus content of the water, and by difference the amount in organic and particulate form was calculated. This never deviated much from the average value of about 20 μg . per litre, and the loss of phosphorus was not therefore accounted for by its removal by phytoplankton. The planktonic flora undoubtedly did increase but the proportion of soluble phosphate so utilized must still have been insignificant. Although there is some evidence that certain species of aquatic macrophytes increased their content of phosphorus as a result of fertilization, the quantity of these macrophytes in the loch was too small to rank as a major factor in phosphate removal. Attached algae which developed as a result of the fertilization contained an appreciable amount of phosphorus, but no quantitative assessment of this community was possible.

The process which probably accounts for the greatest removal of phosphate from the water is chemical adsorption to the bottom deposit. Such a mechanism explains the exponential nature of the decline, provided that the capacity of the surface layer of mud for adsorbing phosphate is considerably greater than the quantity of phosphate actually adsorbed. Laboratory experiments, in which there was no significant planktonic or algal growth, have shown that in such a case the decline is approximately exponential, but the question of the depth of mud which must be involved is still being investigated. In the case of Loch Kinardochy, a depth of between one and two centimetres would be necessary.

To give some impression of the contribution made to the phosphorus content of the mud by the fertilizer added, the following figures are of interest. In the loch concerned, the total phosphorus content in the top centimetre layer of mud was about 220 μg . per square centimetre. Of this, only about 12 μg . would be in an exchangeable form, but the phosphorus adsorbed from the water would contribute another 60 μg . if no other agency was responsible for its removal. The increase in exchangeable phosphate could have a significant influence on biological activity in the region of the mud surface, but this would be dependent on the rate at which the phosphate might be converted to an unavailable form.

The phosphate concentration in the water fell below the limit of detection after about 20 weeks in Loch Kinardochy, but the phytoplankton is believed to have been greatly influenced by the fertilization for the following two years, that is, up to the present time. This will be dealt with in the next paper, where the effect on the normal silica cycle is more appropriately discussed. As far as could be ascertained by frequent analyses, no abnormal changes in the nitrate, ammonia or bicarbonate concentrations resulted from the fertilization. The influence on the bottom fauna is expected to be much slower, and this is still the subject of investigation.

The other fertilizer of importance, as already mentioned, is calcium carbonate. Although calcium hydroxide, as slaked lime, is more readily soluble in water, the high pH resulting from its use causes considerable damage to the flora and fauna, and in any case it has been found to have only a temporary influence on conditions in the water, though probably a more permanent one on the bottom deposit. Calcium carbonate, on the other hand, has no harmful effects, and when added as ground limestone at the rate of half a ton per acre may not produce any significant change in the water generally, though the effect on the mud may be more pronounced. It dissolves very slowly, but the presence of a mud stratum increases the rate of solution to some extent. Results obtained in laboratory experiments involving the addition of limestone to a mud-water system have indicated that, whereas in untreated control experiments the calcium and bicarbonate concentrations increased only slightly, due to leaching from the mud, the addition of limestone produces an appreciable increase in calcium and bicarbonate concentrations. A certain amount of liberated calcium would be adsorbed to the mud. The reaction is obviously slow, these experiments having been followed over a period of two months under static conditions in shallow water. The rate of solution is slower in the absence of the mud stratum. In the deeper and constantly changing water of a loch, no such changes are likely to be observed in the water, but the reaction at the mud surface could nevertheless influence biological activity in that region. The top centimetre of an average acid loch mud might contain only 200 μg . of exchangeable calcium per square centimetre, but the addition of limestone at half a ton per acre is equivalent to 5000 μg . of calcium per square centimetre. As well as providing a considerable potential increase in exchangeable calcium, the flocculating effect which may be produced on the mud particles would assist bacterial activity and the release of nutrients from the mud surface.

The detailed study of the problems discussed has necessitated the designing or modification of analytical methods, particularly in the case of mud analysis. Many other difficulties have still to be overcome, such as that of sampling the mud surface in a manner suitable for providing thin sections for subsequent analysis, bearing in mind that the surface itself is extremely fluid. In this short paper it has been possible to describe only part of the activities of the chemists of the laboratory, but the study of fertilization alone raises many intriguing problems among the complexities of fresh-water chemistry.

SOME BOTANICAL PROBLEMS OF FRESHWATER FISHERIES RESEARCH

By A. J. BROOK.

The addition of superphosphate to Loch Kinardochy has had a remarkable and long term effect on at least its algal flora and much of the botanical work of the laboratory has been directed to following these changes.

Of the three principal algal communities present in lakes—the attached algae, bottom living algae and phytoplankton—only the latter has been studied in detail in this experiment. Prior to the addition of fertilizer, changes in the density and composition of this community were followed in the loch for some $2\frac{1}{2}$ years, from January 1950 to June 1952, samples being taken at fortnightly intervals. This sampling revealed a fairly constant annual pattern of plankton periodicity whose abundance varied between 10 and 100 organisms per ml. In common with other lochs of similar chemical and physical characteristics the winter and spring plankton was dominated before fertilization by flagellates (*Dinobryon* and *Chroomonas*) and diatoms (*Synedra* and *Cyclotella*), each of these organisms attaining their maxima in spring between March and May, after which their numbers declined rapidly. In summer, from June to

August, several species of blue green algae, and *Botryococcus braunii* Kütz and *Stichogloea doederleinii* (Schmidle) Wille, were most abundant, whilst in autumn, though this summer community persisted, flagellates and diatoms once more became numerous and produced small maxima.

After fertilization, the first significant, though short-lived, increase in the phytoplankton became apparent 14 days from the addition of superphosphate and this was dominated by the diatom *Asterionella formosa* Hass, which had previously been found only in very small numbers in the loch. It reached its highest density of 1,030 cells per ml. some 31 days after fertilization but had almost disappeared again fourteen days later. The short duration of this outburst is believed to have been the result of silica depletion, the concentration of this nutrient having fallen well below the value at which diatom growth is considered to be inhibited (0.5 mg./l), for only when the silica concentration returned to a level greater than 0.5 mg./l was there a second increase of diatoms in the phytoplankton population. This, however, was dominated by *Synedra acus* var. *radians* (Kütz.) Hust. which began to multiply rapidly as soon as the silica concentration showed a steady increase above the limiting value in mid-October. This species reached its greatest abundance of 1856 cells per ml. on December 2.

As in previous years, flagellates and diatoms persisted and even multiplied beneath the thick layer of ice which covered the loch for most of the period between November 27 to February 4, the flagellate *Chroomonas acuta* Utermohl attaining an abundance of 3,500 cells per ml. beneath this cover.

During the spring of 1953 there were considerable maxima of *Synedra* and of *Dinobryon cylindricum* Imhof followed by an exceptionally large maximum of *Asterionella* (2,300 cells/ml.), comparable in magnitude to those which occur in the more productive of the English Lakes. An autumn maximum (1,400 cells/ml.) greatly exceeding those usually observed in these productive lakes occurred in late September. A much larger Cyanophycean population than normal also appeared during the summer and autumn in which the colonial *Anacystis montana* (Lightf.) Drouet and Daily, predominated. This was followed by an unusually abundant winter plankton dominated from mid-October until early April 1954 by the colonial green alga *Gemelliscystis neglecta* (Teiling) Skuja in company with lesser numbers of *Anacystis*. *Gemelliscystis* developed two maxima during this period, the largest being in mid-November with a density of 2,600 cells/ml., and a smaller one in February of about 1,500 cells/ml. Its numbers fell rapidly, however, throughout March and its final disappearance was associated with infection of the cells by the fungal parasite *Rhizophidium fulgens* Canter.

The development of *Anacystis* is of interest in that after being abundant in the plankton it later occupied (and in fact continues to occupy) a dominant position in the bottom flora of the loch. The colonies of the alga on reaching a certain size (probably about 2 mm. diam.) sink to the bottom where they continue to enlarge and may attain a size of up to 15 mm. diam. The floor of the loch has been covered with these blue green, jelly-like spheres since early winter 1953 and bottom samples collected in April with a Jenkin Sampler showed densities of about two large colonies per square cm. Wind and wave action roll these gelatinous spheres shorewards and in consequence, many bays of the loch are covered by a deep carpet of the alga. The occurrence of this large growth of *Anacystis* may be the principal reason for the apparent return of the phytoplankton since the spring of the present year at least qualitatively, to its pre-fertilization condition. This year the spring diatom outburst was dominated by *Synedra* followed by *Cyclotella*, as it was before the addition of phosphate in place of *Asterionella*, though possibly all is not over, since the latter species gave rise to a considerable maximum in late August and early September.

Clearly then, the addition of phosphate to Loch Kinardochoy has had a profound effect at least on its algal flora. This in turn appears to have had a considerable effect on the silica content of the loch water, for prior to fertilization this varied from 4 mg./l. in winter to about 1 mg./l. in mid-summer. Within seven days of adding phosphate the concentration of this nutrient had fallen to 0.3 mg./l. while by the beginning of August its value was below 0.1 mg./l., the lowest concentration ever recorded for a loch in this area. Late in August its level rose to a little above 0.5 mg./l. but did not pass the 1 mg./l. level until January. Throughout most of the following year the silica content remained unusually low and from mid-May to early June was below 0.5 mg./l., the value considered to be limiting for diatom growth. After the autumnal diatom maximum, however, its concentration increased rapidly, a concentration of more than 3 mg/l. being maintained from December to April of the present year. Despite the considerably smaller maximum of planktonic diatoms observed this year there was, nevertheless, a rapid and very marked decrease in silica in the spring and again values consistently lower than those normally encountered have persisted throughout the summer. This observation seems to indicate that there has been an increase in the loch of plants other than planktonic diatoms which also utilize silica.

Attention is now being turned to investigating these other plant communities, for while in large lakes (and also in the sea) the phytoplankton constitutes a considerable proportion of their total vegetation, this is not the case in lakes of dimensions which it would be economic to attempt to fertilize. Clearly, the smaller and shallower the loch, the greater will be the importance of the macrophytic vegetation, with its attached algae, and of the bottom living algae which inhabit the mud in the photic zone. Suitable methods have still to be devised for assessing the abundance of these communities.

A further reason why it seems important from the point of view of fisheries biology to investigate these communities in small lochs is that it has been found that the inflowing and outflowing streams may at times wash out their entire plankton crop. Thus assessments of their productivity in terms of the standing crop of plankton can be very misleading.

With these limitations of the value of plankton studies in mind, the possibilities of using attached algal growths as an index of productivity are being explored. Quantitative collections of these algae, which usually include stalked diatoms, many of the prostrate systems of members of the Chaetophorales and a variety of filamentous algae, are made by suspending microscope slides in lochs at given depths for a standard time. Work is progressing on determining the abundance of the growths which settle on these substrata in terms of their photosynthetic activity and chlorophyll content.

One more reason why it seems important to study this attached community in detail, in preference to the phytoplankton, is that whilst we know little about what eats the latter, we do know that many attached algae form a considerable part of the food of insect nymphs and larvae, and these in turn are most important as trout food. Under natural conditions they occur in considerable abundance on submerged macrophytes, being particularly plentiful on such species as *Myriophyllum spicatum* L. and *Eleogiton lacustris* (L.) Link. In collaboration with the laboratory's entomologist, studies have been made on the value which different species of algae may have as food for these larvae. For example, mayfly nymphs, *Leptophlebia vespertina* L., which had been fed exclusively on filamentous diatoms have doubled their length in 52 days while others fed on cultures of *Botryococcus*, *Oscillatoria* and various species of Chlorococcales grew but little, and in fact appeared to be unable to digest these forms. Such observations suggest that not only is the amount of algal food important but also its nature. Thus from the point of view of fertilization experiments the aim must be at quality as well as quantity.

THE SELECTION OF SPAWNING SITES BY TROUT

By T. A. STUART.

Before describing the field and laboratory investigations which have recently been carried out on the factors affecting the selection of spawning grounds by trout, the spawning process will be briefly described.

Trout lay their eggs in nests, or redds, which lie within gravel of a suitable size and which are excavated by the female. Excavation occurs as a result of the currents set up by the 'cutting' movements of the tail of the female and when a pit of sufficient depth has been formed, the eggs are laid into it and are fertilized immediately by the attendant male. The female then moves a short distance upstream and covers the eggs with gravel, again by means of currents set up by the movements of her body. After hatching, the alevins remain within the gravel until most of the food supplies in their yolk sacs have been consumed and they then emerge into the water.

Rivers vary in volume and velocity and suitable sites for spawning are not generally available over the whole area of the river bed. They occupy special positions in relation to the topography of the river bed and are primarily dependent on deposits of gravel of a particular composition and well-defined size range.

In some rivers almost every pool provides adequate spawning ground sometimes in excess of the requirements of the stock of fish. In such cases, from our knowledge of the high efficiency of the trout redd, a simple count of spawning fish, or in special circumstances, knowledge of the amount of the total population, is sufficient to enable a reasonable estimate to be made of the number of fry hatching out each season. At the other extreme, complete absence of suitable gravel deposits makes assessment even more simple—no reproduction at all is possible and artificial stocking must be the sole means of replenishing stocks. The great majority of trout streams of course provide spawning facilities at all levels between these extremes. Most of them have gravels of varying quantity, composition and degree of cleanliness, *i.e.* freedom from mud, silt and sand which, if present in excessive amounts, would destroy the ova buried in the gravel. If such a typical stream is examined it is found that while the trout select certain areas for spawning they pass over others which superficially may appear to be of similar character to those selected.

At an early stage of the investigation, after many ripe fish had been observed consistently to pass over certain banks of gravel to occupy instead other areas which to the casual human eye showed no difference on the surface, these banks were examined more critically. It was found by digging into them that beneath the surface of relatively clean gravel the whole bank was consolidated by heavy deposits of silt and mud. As is known from experiment and much practical experience in hatcheries, such conditions would preclude any possibility of trout ova surviving should they be deposited in such sites. But no fish ever excavated to investigate by vision or any tactile sense the suitability or otherwise of such sites and redds were never made there.

As the surface appearance of the gravel banks gave no obvious indication of the suitability or unsuitability for redd making, an attempt was made to investigate the means whereby the fish unerringly choose a favourable site. Further observations made during spawning runs showed that the ascending fish, after passing into a spawning pool, stopped abruptly at the exact site where eventually (within a few minutes or perhaps several hours) it commenced the excavation of the redd.

The only possible source of information to the fish regarding the suitability of the site appeared to be the presence of a downward current of water which was considered to be necessary for the survival of the ova. Accordingly, to test this theory, crystals of soluble dyes were placed on the surface of several

gravel banks including some which were never used as sites for redds. It was immediately apparent that on the suitable grounds (as selected by the fish) a positive downward current was rapidly removing the dye allowing little or none to travel directly downstream, while on the gravels which were consolidated by mud and silt all the dye flowed over the surface. It was also found that the dye introduced on the surface of the permeable gravel emerged a few seconds later at the downstream end of the bank where one pool gave place to the next.

A further test was now carried out to demonstrate the positive nature of this important downward current. A freshly killed trout which weighed about 270 g. in air was suspended in the current running through the pool by a fine nylon thread about 10 feet in length which was attached to the closed mouth of the fish. The other end of the thread was fixed to the arm of a specially designed spring balance which was kept at a constant level above the surface of the water. The spring balance thus measured roughly the resistance of the body of the fish to the current flowing through the pool. This resistance differed in different places in the pool as the fish was towed against the current, but the dead fish, as it was pulled over the site normally selected by living fish for spawning, sank abruptly to the bottom and remained there offering no measurable resistance to the current flowing rapidly over it. In all these experiments it was observed that the dead fish maintained the normal orientation of the living fish and came to rest with outspread pectoral fins on the site where resistance was at the minimum. Indeed the attitude of the dead fish at this place was indistinguishable from that of a living fish.

This experiment suggested that the ripe fish passing over such an area on its journey upstream must become immediately aware of a downward current which cancelled out, at least partly, the force of the stream. It also seemed likely that such sites were the only possible ones where the operation of redd-making could be carried out. This operation involves the fish in a leisurely 'testing' of the site at each stage in the excavating of the redd which would be almost impossible to accomplish in face of the full force of the downstream current. It may at least be considered fortuitous that such sites selected by the fish in this manner are the only ones in the pool where the ova could hatch or the larvae develop successfully.

Following upon these field observations and experiments a model of a typical spawning pool was constructed in a laboratory tank with transparent sides measuring 6 ft. by 1 ft. by 1 ft. The introduction of dyes, etc. enabled the currents within the gravel to be seen and the use of specially designed manometers enabled the relative strength of these currents to be measured in relation to the rate of water flow through the tank.

It was possible to demonstrate, using this model, that the downward currents were always at right angles to the surface of the gravel and that their force was at a maximum value near the apex of the gravel mound. It was also shown that these currents within the gravel are relatively constant in strength at all normal rates of flow, though they decrease somewhat during spates and increase when the rate of flow is low, *i.e.* at minimum summer levels. Later, a pair of ripe trout were introduced into the artificial pool. The female selected the site for her first redd near the top of the gravel mound as predicted from a knowledge of the currents within the gravel and successive pockets of ova were deposited at short distances in an upstream direction. This experiment was repeated and, in all, eight pairs of trout spawned in succession in this pool. The location of each pocket differed only in a lateral direction and by not more than two inches.

A knowledge of the conditions associated with gravels suitable for the construction of redds has made it possible to predict accurately the sites which will be selected by spawning fish in a stream and it has also been found practicable to alter unsuitable gravels so that trout were able to utilize them for

spawning. It would therefore seem likely that these observations could have considerable practical importance in assessing the potential spawning grounds in a stream.

THE CAPACITY FOR FLIGHT OF CERTAIN WATER BEETLES AND ITS BEARING ON THEIR ORIGIN IN THE WESTERN SCOTTISH ISLES

By DOROTHY J. JACKSON, F.R.E.S., F.L.S.

(With Plate 7 and 8 text-figures.)

In a recent paper F. Balfour-Browne (1953) listed the aquatic Coleoptera of the Western Scottish Isles and discussed their origin and means of arrival.

He concluded that these islands have been stocked by a constant immigration of water beetles from Scotland and Ireland and in some cases from an even greater distance. This assumes that the species concerned are capable of flight.

In the present paper this conclusion is discussed in the light of the investigations which I have been making into the capacity for flight of water beetles.

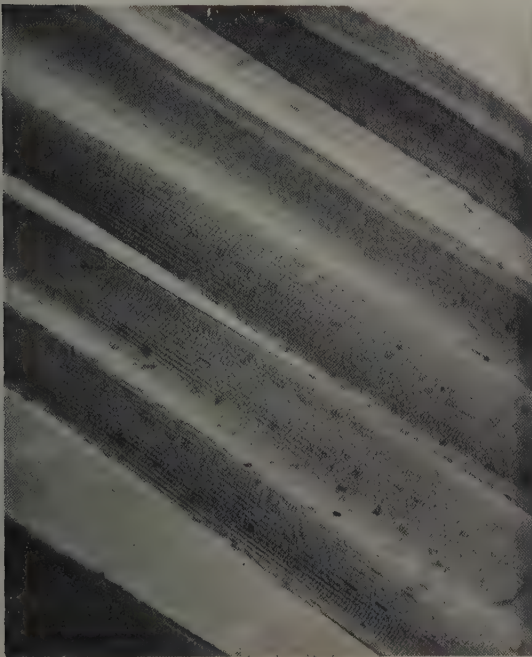
Balfour-Browne also dealt with the question of the possible extension of range of certain species within the British Isles, and this aspect of distribution will be considered first.

EXTENSION OF RANGE IN THE BRITISH ISLES.

Balfour-Browne's view that certain species are extending their range in the British Isles also presupposes flight as a means of dispersal. In numerous areas of Scotland there has been little or no systematic collecting of aquatic Coleoptera so that it would be unwise to conclude that an unusual species recently collected in such an area is necessarily a new arrival.

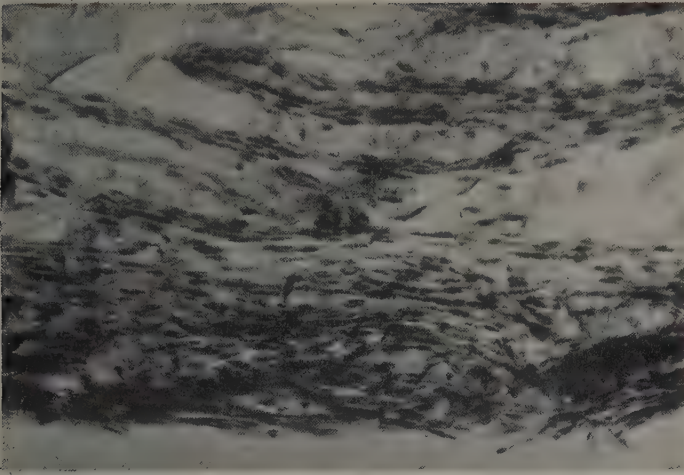
It is probable that the strongly flying species do extend their range but we know little of the conditions which stimulate water beetles to natural flight, though in the tests which I have carried out (1952, a) warm weather or artificial heat appeared to be essential. Overcrowding alone cannot be the stimulus as one frequently finds scores of water beetles, including those that are good fliers remaining in a small pool in which the water is drying up. Even in dried up pools *Agabus bipustulatus* L. is found under stones (Jackson, 1952 a, S. E. Allen, 1954). This species is a good flier and has often flown in tests. I have dissected over one hundred specimens and all have had fully developed flight muscles (Pl. 7, fig. 1). The wide distribution of this species which is tolerant of all sorts of habitats, from pools at sea level to mountain lochans, and its frequent occurrence in temporary waters, also indicate ready dispersal, so that there can be no doubt that individuals fly at certain times. Other species which fly readily and are widely distributed will doubtless also extend their range by flight and examples of such species have already been listed (Jackson, 1952 a). However there are many species, which, though capable of flight, have a limited distribution in the British Isles, even in southern districts. The tendency to disperse by flight will be rigorously controlled by natural selection in those species which can only thrive in a restricted type of habitat.

As well as the dispersal of strong flying species by their own efforts small water beetles, if capable of flight, may possibly be carried by air currents, as



1

mm.
0.2
— 0.1 —
0



2

FIG. 1.—Some fibres of normal flight muscle of a mature male of *Agabus bipustulatus* showing nuclei and cross striation. Fixed Carnoy's Fluid, stained Delafield's Haematoxylin; Objective 5, Eyepiece 10, Malcam Camera attachment.
FIG. 2.—Part of an abnormal flight muscle showing numerous fibres with elongated nuclei, from an almost mature female of *Platambus maculatus*. Same fixative and staining.

Balfour-Browne suggests. Berland (1937) has observed that insects of small size, rarely more than 2 or 3 mm., such as Aphids, Psyllids, Thrips, etc., which are mostly weak flyers or even wingless (Collembola), may be passively transported as plankton of the upper air. Perhaps weak flying Halipids may be spread over short distances in this manner, and the single specimen of *H. obliquus* F. which I took in August 1951, in a well worked artificial pool in Fife (1952 b) may have arrived from the air. Berland concludes that all insects of good size and those capable of flight are confined to the soil and to the lower 'terrestrial' zone of the atmosphere (not exceeding perhaps 100 metres of thickness) not only by their own weight, but because they have the power to resist physical agents which tend to detach them. Berland's observations refer presumably only to land insects and it seems very improbable that beetles could be swept out of water by whirlwinds and be transported, still living, to colonize distant waters, and I agree with Balfour-Browne that flight is associated with the idea of wind transport. Flight is also believed by Palmén (1944) to be the initial cause of the arrival of windborne insects in mass flotations on the coasts of Finland.

There can, however, be no question of the recent arrival of the two species of *Noterus** which I took in two lochs in Fife on my first visit to them in 1949, though Balfour-Browne (1952, 1953) cites these records as evidence of recent extension of range. He does not mention the facts I have already recorded (1950), firstly, that all the specimens (total number now 90) of the smaller species, *N. crassicornis* Müll. which I have examined from Lindores Loch had short wings quite useless for flight, and secondly that all the specimens (25) of the larger species, *N. clavicornis* De Geer, from Kilconquhar Loch, which I dissected were without normal flight muscles. In a later paper (1952 a) I referred to the modifications of the phragmata and muscle discs of the metathorax in certain water beetles in which the flight muscles are undeveloped, and these modifications are well shown in the *N. clavicornis* from Fife. Both species are well established in these lochs (one species only has been found in each loch) and I have taken them on several subsequent visits. They are usually common in the spring and autumn, but on some days they are very scarce and occasionally I have got none, but it would be rash indeed to conclude, on the unlucky collecting days, that they were absent from the lochs. In my opinion these species have been established in these lochs (which date from the closing stages of the Glacial Period) for a very long time, and they probably reached the lochs at a time when much of the country was marshland and swamp and when even a flightless water beetle would have a chance to extend its range. It is already clear from the investigations I am making of material kindly supplied to me by many entomologists that the flightless form of *N. clavicornis*, and the brachypterous form of *N. crassicornis* are widely distributed in Great Britain and in Europe. From over 170 British specimens of *N. clavicornis* dissected, only two (from the south of England) have had fully developed flight muscles and large phragmata and muscle discs; on the Continent the proportion appears to be rather higher. In *N. crassicornis* no normal flight muscles have been found in any specimen, not even in those with larger wings. The wide distribution of the flightless forms indicates that the tendency to flightlessness in these species is no recent development but goes back to a remote period.

* The names of our two species of *Noterus* as formerly used by British entomologists are at variance with the names used for the same species on the Continent (Jackson, 1954, *Entomologist's Gazette*, 5, 63). Owing to the discovery that De Geer's specimens of *clavicornis* are the larger species, as reported by Dr. Guignot in 1946 (*Bull. Soc. ent. France*, 1946, p. 75), it is clear that the British nomenclature is wrong. This has been confirmed by Mr. J. Balfour-Browne who has recently seen De Geer's specimens. The correct names as used in this paper are: for the larger species: *clavicornis* De Geer, in place of *capricornis* Herbst, and for the smaller species *crassicornis* Müller, in place of *clavicornis* Deg.

SPECIES OCCURRING IN THE WESTERN ISLES.

In Balfour-Browne's list of 93 species from the Western Isles there are a number of species for which so far I have no evidence that flight is possible, all the specimens which I have dissected being without normal flight muscles and showing corresponding modifications of the metathorax, and in some the wings may be reduced in size. Other species are variable in regard to the development of the flight muscles, and in 34 species all the specimens I have dissected have had normal flight muscles.

I am very grateful to the various entomologists who have sent me specimens, recorded under their initials in the following notes. Where no initials are inserted I have myself collected the specimens. Specimens mentioned in this paper have been received from Professor F. Balfour-Browne, Mr. J. Balfour-Browne, Dr. G. W. R. Bartindale, Professor K. Berg, Dr. K. G. Blair, Mr. P. Blasdale, Mr. E. S. Brown, Mr. L. Christie, Mr. G. L. Frewin, Mr. F. D. Goodliffe, Dr. F. Guignot, Mr. W. Hellén, Professor J. W. Heslop Harrison, Dr. H. B. N. Hynes, Dr. T. T. Macan, Mr. J. A. Owen and Dr. R. Richter. In addition Professor C. H. Lindroth has most kindly sent me many water beetles from Sweden preserved in alcohol and those included here were collected by C. Roth from 1855 to 1887. I am much indebted to Professor J. W. Heslop Harrison for advice in biogeographical problems and to Mr. J. Balfour-Browne and to Mr. E. B. Britton for helpful criticism in regard to the recording of my results.

Species of which only Flightless Forms have as yet been observed in Britain.

Some particulars have already been given of the species so far found to be without normal flight muscles (1952 a) and all the evidence now available is given here on the species of this class which occur in the Western Isles. A full account of the wings, flight muscles and their skeletal supports in a flying *Agabus* and the reduction of these parts in a flightless species has now been completed and is ready for publication, so only brief notes will be given here of the anatomical differences observed.

The principal modifications of the metathorax in the flightless beetles consist in the shortening of the metatergum from prescutum to postnotum (in some Dysticidae), a partial reduction of the prephragma* and postphragma, to which the median metathoracic muscles—indirect flight muscles—are attached, and a reduction in size of the subalar and basalar discs of the pleural flight muscles. In such specimens the flight muscles when present are greatly reduced in size and are usually surrounded with fat body. They consist of very narrow fibres which are crowded with elongated nuclei and there is no cross-striation (Pl. 7, fig. 2).

Hygrotus 9-lineatus Steph.

Fifteen specimens have been dissected from Kinross, Elgin (R. R.), Argyll (Main), Inverness (East), Cumberland (T. T. M.), and some with no data of locality (F. B. B.), also two from Kvie Sö, Jutland, Denmark. In none have normal flight muscles been found, in some the flight muscles were intermediate in development between normal and abnormal muscle, in other specimens no flight muscles at all were found. The discs of the pleural flight muscles were fairly large. Balfour-Browne (1915) comments on his failure to find this species in the Outer Hebrides. He lists (1953) one record each for the North and Mid Ebudes. As it is principally a loch species, and as its capacity for flight is somewhat doubtful, it is not likely to disperse freely.

* In some flightless Hydroporini the prephragma shows less reduction than the postphragma though there are no median metathoracic muscles to support. It has evidently persisted to give support, by its anterior surface, to a longitudinal muscle of the mesothorax.

Deronectes assimilis Payk.

For this species, classed by St. Claire Deville (1930) as boreo-alpine, Balfour-Browne lists eleven records, six from the Outer Hebrides and the rest from the North and Mid Ebudes. I have dissected 40 specimens, from Elgin (R. R.), Fife, Argyll (Main), Inverness (East) and Kirkcudbright, specimens of all ages, but in none have normal flight muscles been present. The metatergum is a little shorter and the discs of the pleural flight muscles are much smaller than in *D. griseostriatus* Deg. (Elgin, R. R.), fig. 1, in which I have found normal flight muscles.

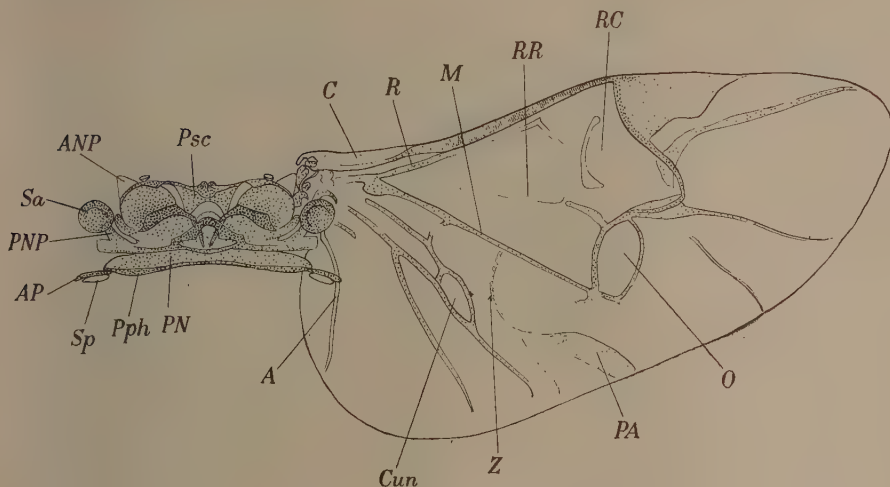


Fig. 1



Fig. 2

FIG. 1.—*Deronectes griseostriatus* Deg. Wing and metatergum, internal view, with subalar disc *in situ* but rest of pleuron removed. From ♂ collected Loch Allan, Elgin by Dr. R. Richter, 24.ix.50. Normal flight muscles. $\times 15.7$.

FIG. 2.—*Deronectes elegans* Panz. Wing and metatergum, internal view, with subalar disc *in situ*. From ♂ with abnormal flight muscles, collected Prior Muir, near St. Andrews, 14.iv.51. $\times 15.7$.

For explanation of lettering see page 94

Deronectes depressus-elegans F.*

Balfour-Browne remarks that this species, which occurs in the Inner Hebrides, has a very limited range in the islands, considering its wide distribution in Britain. I have dissected 34 specimens of various ages (all of the form *elegans* Panz.) from Orkney (F. B. B.), Inverness (East), Fife, Kinross, Argyll (Main), Berwick, North-West Yorks (T. T. M.), Cumberland (T. T. M.) and Cheshire (G. W. R. B.). All had abnormal flight muscles or no flight muscles and small pleural discs. A few examined from Sweden and from Denmark were also without normal flight muscles but in some of the Swedish specimens the discs were larger than in the British specimens.

The wings of *D. assimilis* and of *D. elegans* (fig. 2) are smaller than the wings of *D. griseostriatus*, with normal flight muscles, from Elgin (fig. 1) though the two latter species are approximately of the same size. Several specimens of each species, where possible from different localities, have been compared, the wings and metatergum being mounted flat (as in the figures) and measured with an eyepiece micrometer. The results are recorded in Table I. It will be seen that in *D. assimilis*, a slightly smaller species, the wings measured from 3.8 to 4.2 mm., in *D. elegans* from 3.9 to 4.6 mm., but in *D. griseostriatus* the wings were 5.6 mm. In all three species the width of the metatergum varied within the same limits, indicating that the individuals were of approximately similar width. The length of the metatergum in the two apparently flightless species is however noticeably less than in *D. griseostriatus*. In *D. assimilis* and *D. elegans* there is thus, in addition to the absence of normal flight muscles and the modification of the metatergum and the pleural discs, a definite wing reduction; once the flight muscles have failed to develop normally, other regressive changes have probably set in, since the presence of normal wings, in a species unable to use them, will no longer be of selective value. In assessing capacity for flight it is desirable to compare the supposed flightless species with normal 'flying' species of the same genus. A small reduction in wing size alone is not a sufficient criterion, but combined with the other modifications, flight in such individuals must be impossible. In some of the larger flying Dytiscidae the wings are not very large relative to the size of the insect, but they are controlled by large and powerful flight muscles with strongly developed sclerotic supports.

Oreodytes rivalis Gyll.

Balfour-Browne remarks that this species is decidedly scarce on the Western Isles and also on the western mainland. I have dissected 13 specimens, both soft and mature, Elgin (R. R.), Inverness (East), Fife and Kinross. All are without normal flight muscles.

Hydroporus morio Dej.

Thirty-one dissected, Inverness (East) (J.A.O., D.J.J.), Fife and Perth (Mid.). No normal flight muscles were present and even abnormal flight muscles were rarely found. The pleural discs are usually very small, and the wings of a few specimens which I have measured are smaller than in *H. nigrita* F., a slightly smaller species which has normal flight muscles and is capable of flight. *H. morio* is recorded from the Inner Hebrides but it appears to be rare in the Outer Hebrides (Balfour-Browne, 1915, 1953). It is a local species and probably flightless.

* Balfour-Browne uses this name in his *Handbook for the Identification of British Insects, Coleoptera, Hydradeephaga*, 1953. In his Western Isles paper (1953) he refers to this species as *depressus* F., though he records the form *elegans* Panz. from Skye (1911, *Ann. Scot. Nat. Hist.*, 212) and from the South Ebrudes (1923, *Scot. Nat.*, 55-60: 87-93).

TABLE I. Size of wing and metatergum in species with and without normal flight muscles. (No soft specimens have been used for these measurements).
The size of the species is that given by W. W. Fowler (1887).

Species.	Width of metatergum, from wing base to wing base by anterior notal wing process.	Length of metatergum from prescutum to postnotum.	Length of wing.
<i>Dronectes assimilis</i> Payk (No normal flight muscles). Size $4\frac{1}{2}$ by $2\frac{1}{2}$ mm.	mm.	mm.	mm.
♀, pond, Kettlehill, Fife, 5.v.53	1.5	0.4	3.8
♂, Loch Allan, Elgin (R.R.), 24.ix.50	1.5	0.5	4.0
♂, pond, Prior Muir, Fife, 14.iv.51	1.5	0.4	4.1
♂, Loch Garten, Inverness-shire, 9.vi.52	1.6	0.4	4.2
<i>D. depressus-elegans</i> F. Form <i>elegans</i> Panz (No normal flight muscles). Size $4\frac{1}{2}$ by $2\frac{1}{2}$ mm.			
♂, pond, Prior Muir, Fife, 14.iv.51	1.5	0.4	3.9
♂, River Ure, Aysgarth, Yorks (T.T.M.), 28.viii.53	1.5	0.4	3.9
♂, "Derwent" Water, Cumberland (T.T.M.), 9.x.53	1.6	0.4	4.1
♂, ditch near St. Andrews, 28.vii.51	1.5	0.4	4.2
♀, North Rode, Cheshire (G.W.R.B.), 30.viii.53	1.6	0.5	4.4
♂, stream near Longformacus, Berwick, 16.vi.51	1.6	0.5	4.4
<i>D. griseostriatus</i> Deg. (Well developed flight muscles). Size $4\frac{1}{2}$ by $2\frac{1}{2}$ mm.			
♂, Loch Allan, Elgin (R.R.), 24.ix. 50	1.5	0.8	5.6
♂, " " " " " "	1.6	0.8	5.6
♀, " " " " " "	1.6	0.8	5.6
<i>Hydroporus ferrugineus</i> Steph. (No normal flight muscles). Size 4 by 2 mm.			
♀, Tynet Burn, Elgin (R.R.), 28.v.51	1.4	0.4	3.3
♀, " " " " " " 29.v.51	1.5	0.4	3.5
♂, " " " " " "	1.5	0.4	3.6
<i>H. planus</i> F. (Well developed flight muscles). Size $4-4\frac{1}{2}$ by $2-2\frac{1}{2}$ mm.			
♂, Goldings Wood Pond, Herts (E.S.B.), 25.xi.49	1.6	0.6	5.2
♀, pool, Seafeld, St. Andrews, 15.ix.50	1.5	0.6	5.4
♂, cattle trough, St. Fort, Fife, 24.xii.49	1.4	0.7	5.6
<i>H. pubescens</i> Gyll. (Well developed flight muscles). Size $3\frac{3}{8}$ by $1\frac{1}{2}$ mm.			
♀, pool, Kippo, Fife, 2.i.50	1.2	0.5	4.2
♂, Moss Morran, Fife, 27.ix. 50	1.2	0.5	4.2
♀, pool, Guardbridge, Fife, 18.ix.50	1.2	0.5	4.3
<i>H. melanarius</i> Sturm. (No normal flight muscles). Size $3-3\frac{1}{2}$ by $1\frac{1}{2}-1\frac{3}{4}$ mm.			
♀, Moss Morran, Fife, 23.x.53	1.1	0.32	3.0
♀, " " " " " "	1.2	0.35	3.1
♂, " " " " " "	1.1	0.32	3.2
♀, Above Glen, Lyon, Perthshire, 15.viii.53 ..	1.0	0.39	3.5

Hydroporus obscurus Sturm.

Balfour-Browne remarks on the wide distribution of this species on the islands. I included it in my list of specimens so far found with imperfectly developed flight muscles or no flight muscles and with the discs of the pleural flight muscles small (1952 a). I have now dissected 31 specimens from Fife, Perth (Mid), Inverness (East), Raasay, and Argyll (Main), and all are of this character. The wings, though of full size, are very fragile and weakly veined. I have recently dissected some Swedish material (C. H. L.), 12 specimens taken in May 1870, at Sk. Ringsjon, and I am much interested to find that in seven, normal, well developed flight muscles are distinct and the pleural discs are larger and the wings more strongly veined than in the Scottish specimens. Even if flying specimens do exist in Scotland it seems open to doubt that such a small species, a denizen of sphagnum pools and moorland lochs, should have successfully migrated from the mainland to become established in 25 of the Western Isles, a feat which many good flying species have apparently failed to accomplish.

Hydroporus ferrugineus Steph.

Balfour-Browne notes two records of this rare species, one specimen from Mull and one from St. Kilda, and he states: "There is no doubt that the two specimens recorded from the islands were wanderers from the mainland or even from Europe, just as many examples taken in Britain may have come from the continent". This is a very local species, frequenting springs, and unfortunately I have had only four specimens for dissection, three from Elgin (R. R.), and one from Berwick, but in these there is no trace of flight muscles, the metatergum is feebly sclerotic, and shorter, measured from prescutum to postnotum, than in a flying species of comparable size, the pleural discs are very small, while the wings also are considerably smaller than in a 'flying' *Hydroporus* of similar size. I have made measurements of the metatergum and wing in three specimens of this species and compared them with two other species both of which I have always found to have perfect flight muscles and to be ready flyers, these are *H. pubescens* Gyll., a smaller species, and *H. planus* F., a species of about the same size as *H. ferrugineus* or slightly larger. The measurements are recorded in the table.

While some variation occurs in the size of the wings in the different individuals, the wings of *H. ferrugineus* (fig. 4) are smaller than either of the other species (fig. 3). In these specimens of *H. ferrugineus* flight reduction has reached the stage of wing reduction (even more markedly than in *Deronectes elegans*) and the likelihood of such an insect flying from the mainland to St. Kilda, or even to Mull, seems very improbable. It is more likely that this species, which Guignot (1933, p. 964) classes as subalpine, has inhabited its present localities since the time of land connections, perhaps in springs or underground waters.

Hydroporus melanarius Sturm.

Recorded from both the Outer and Inner Hebrides. In Fife this species appears to be very uncommon. I have taken it only in one locality on Moss Morran, on two visits. I have dissected seven specimens from there, all without normal flight muscles and with small discs and modified metatergum and rather small, frail wings. A specimen from Perthshire, also without normal flight muscles had larger discs and wings. See Table I.

Agabus guttatus Payk.

I have dissected 26 specimens from Fife, Elgin (R. R.), Perth (Mid.), Raasay, Berwickshire, Herts (E. S. B.), also one from Baden, S.W. Germany (R. R.) and two from Sk. Ringsjon, Sweden (C. H. L.) taken in June 1860. In none

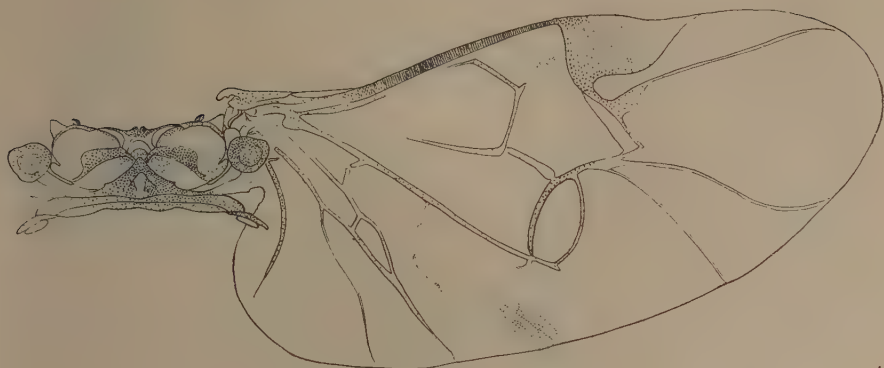


Fig. 3



Fig. 4

FIG. 3.—*Hydroporus planus* F. Wing and metatergum, internal view, with subalar disc *in situ*. From ♀ taken near St. Andrews on 15.ix.50. Seen to fly. Normal flight muscles. $\times 17.8$

FIG. 4.—*H. ferrugineus* Steph. Wing and metatergum, internal view, with subalar disc *in situ*. From ♀ taken by Dr. Richter in Tynet Burn, Elgin, 29.v.51. No flight muscles. $\times 17.8$

have normal flight muscles been found, but in some the flight muscles are intermediate in character between normal and abnormal flight muscle. This species, classed by Guignot as subalpine, frequents small streams and trickling waters. I have taken it commonly around St. Andrews, and in one stream I found it under stones together with *A. biguttatus* Oliv., but whereas the latter species has well developed flight muscles and flies readily, *A. guttatus*, though tested repeatedly, has never been seen to fly. *A. biguttatus*, which is rare and local, is only recorded from Rhum, but *A. guttatus* is listed with seven records from all four groups of the Western Isles.

Agabus congener Payk.

More specimens of this species are required. Only a few have been available, not all well preserved. Though none of these showed normal flight muscles the pleural discs were variable in size and the flight muscles, when distinguishable showed either abnormal or intermediate characters. From Finland, three specimens have been sent me (W. H.), in two of which normal flight muscles were present, but in the third specimen no flight muscles were found and the discs were small.

Platambus maculatus L.

This species is only recorded from two localities in the North Ebrides and one in the Outer Hebrides. I have dissected 91 British adults of all stages of maturity; from Inverness (East) (G. L. F.), Elgin (R. R.), Argyll (Main), Perth (Mid.), Fife, Midlothian (J. A. O.), Berwick (J. A. O.), Dumfries (F. B. B.), Westmorland (K. G. B., T. T. M.), Lancs. (North) (T. T. M.), (Yorks (Mid-West) (H. B. N. H.), Yorks (North-west) (T. T. M.), Cheshire (G. W. R. B.), Denbigh (H. B. N. H.), Caernarvon (H. B. N. H.), Suffolk (K. G. B.), Middlesex (K. G. B.), Surrey and Devon (K. G. B.). In none were normal flight muscles present, in many no flight muscles were found, and in the rest very thin fibres of abnormal histology were present, Pl. 7, fig. 2. The metatergum in all specimens is shorter than in a flying species of *Agabus* of similar size and the pleural discs are usually quite small. Moreover in all those specimens in which the wings have been mounted flat, it is clear that the wings are smaller than in a 'flying' species of comparable size, e.g. *Agabus chalconatus* Panz. A few specimens have been received from the Continent, from Sweden (C. H. L.), Denmark (K. B.), Germany (R. R.), Finland (W. H.), and France (F. G.). In these no normal flight muscles were found and the metathorax showed the same structure as in the British specimens, but the wings of some of the continental specimens are wider. I do not know of any record of this species having been observed in flight. Balfour-Browne (1953) refers to the occasional occurrence of this species out of water. Mr. Owen found a few specimens resting on a log in a pool in a stream in Berwickshire. They were in the sunshine and the elytra were quite dry. He most kindly sent me the specimens, well preserved in alcohol, and, on dissecting them I found them to present the same evidence of incapacity for flight as all the others. I have little doubt that this species is flightless in Britain and possibly also on the Continent.

Dytiscus lapponicus Gyll.

This is a boreo-alpine species, considered by Sharp (1901) and Rüschkamp (1926) to be a glacial relict of northern origin. It is known from both the Inner and Outer Hebrides and from various parts of the Scottish Highlands, Orkney and Arran (Balfour-Browne, 1950). It has a curiously local distribution. Thus, on the Isle of Eigg, D. K. McE. Kevan (1941) found it abundant in July 1939, in one small lochan where it had long been known, but he states that "it does not appear to inhabit any other loch on the island". J. W. Heslop Harrison (1940) found it widely distributed on the Island of Raasay, both in lochs and shallow moorland pools.

Only a few specimens of this interesting species have been available for dissection and I would be very glad to receive more, alive or in alcohol. I have dissected two specimens (dried) from Arisaig, one of them soft, August 1952 (J. A. O.), one (dried) from Raasay, August 1936 (J. W. H. H.), and two (dried) from Eigg, July 1939, collected by the expedition from Edinburgh University and kindly sent to me by Mr. A. R. Waterston. In dried specimens of flying beetles the flight muscles show for many years but none were to be found in these *D. lapponicus*, though the leg muscles were distinct.

Dissection of three specimens from Cnoc Sasunnaich on the boundary of Sutherland and Ross-shire, 1948 (J. B. B.), which were well preserved in Pampel's Fluid, showed that the space in the metatergum occupied in other *Dytiscus* by the voluminous fibrous flight muscles, was filled with fat body. In one beetle, abnormal flight muscles were found embedded in the fat body; the best developed muscle was attached to one subalar disc. This muscle was stained in Delafield's haematoxylin and mounted in Euparal, and shows narrow fibres from 9 to 12 μ in diameter, with long rows of elongated nuclei, and no cross-striation. The normal fibres of the same flight muscles in *D. marginalis*, preserved in alcohol, and similarly mounted, measure from 100 to 120 μ . In the other two *lapponicus*, after careful teasing apart of the fat body, not even abnormal flight muscles could be identified with certainty, but all the tubular muscles were well developed.

Very striking are the modifications of the metathorax in all eight specimens. I have compared them with specimens of *D. semisulcatus* Müll. which I took in Raasay and which have enormous flight muscles, still recognizable though the specimens had been put aside to set and had been left for nearly six months relaxing! In *semisulcatus* the metatergum has very prominent prephragmal lobes and the postphragma is also strongly developed, the internal ridges of the metatergum have transparent shelf-like extensions, and the discs of the pleural flight muscles are large and consist of a sclerotic central area and a broad transparent margin. The metatergum measures 4.8 mm. long. In large specimens of *lapponicus* of approximately the same size, the metatergum is only 3.6 mm. long, the prephragma and the median area of the postphragma are undeveloped, the internal ridges of the metatergum are unextended and the pleural discs are smaller. Moreover, in those specimens in which I have succeeded in unfolding the extremely brittle wings, these are considerably smaller than in *semisulcatus*, when specimens of the same size are compared.

In six freshly killed, mature, specimens which I collected near Arisaig in June 1954, the abnormal flight muscles show clearly. They are better developed than in the Cnoc Sasunnaich specimens and are quite voluminous since the narrow individual fibres are spaced apart and much fat body occurs between them, supported also by numerous tracheae. The fibres are not cross-striated and they are not doubly refractile in polarized light with crossed Nicols, as are the leg muscles, or the normal flight muscles of other species. In these *lapponicus* the chitinous supports of the flight muscles show little better development than in the specimens already described, so I conclude that the flight muscles have never attained full development but have served to enclose a reserve of fat body.

I have dissected some specimens from Lund, Sweden, collected in May 1855, by C. Roth (C. H. L.), and well preserved in alcohol. One, a female, with mature ova, had apparently normal flight muscles, but the fibres measured only 30 to 45 μ . Some fibres showed cross-striation and were doubly refractile in polarized light with crossed Nicols. The character of the metathorax approached that of *semisulcatus*. The other Swedish specimens had the flight muscles abnormal, though the leg muscles were well preserved; the metathorax was variable in development.

These observations suggest that incapacity for flight may be responsible for the present local distribution of Scottish *lapponicus*, but it would be interesting to know if forms with as well developed flight muscles as the Swedish specimen also occur and are perhaps responsible for the wider distribution of this species in some areas.

Orectochilus villosus Müll.

The only specimens I have examined are one from Argyll (Main), one from Sweden (C. H. L.), and 25 from Germany (R. R.). All have such short wings relative to their long bodies that it is doubtful if they could fly. Larsén (1954) is in agreement with this view. The striking contrast in the size of the wing in this species as compared with the wing of *Gyrinus natator*, a ready flier, is shown in figs. 5 and 6, in which the wings of two beetles of almost the same size are compared. Balfour-Browne lists two records of *O. villosus* from the Mid Ebudes.

Anacaena globulus Payk.

Well represented in the Western Isles. I have dissected 75 specimens from Elgin (R. R.), Fife, Inverness (East), Argyll (Main), Raasay, Berwick, Kirkcudbright and Surrey, and two from Denmark. None had flight muscles, and the pleural discs are very small. Yet in the allied species *A. limbata* F., perfect flight muscles and good sized discs have been found in 28 specimens, both British and Danish, and only in two specimens were the muscles absent and the discs small.



Fig. 5A

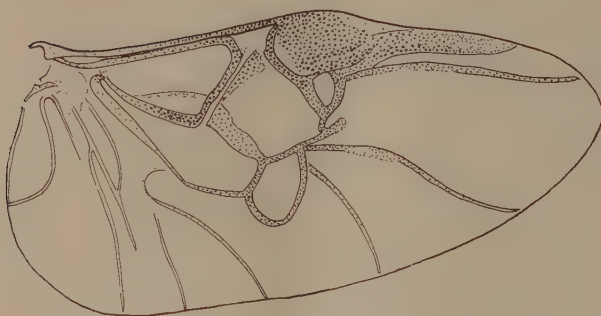


Fig. 5



Fig. 6A

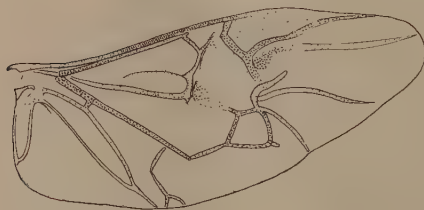


Fig. 6

FIG. 5.—*Gyrrinus natator* L. var. *substriatus* Steph. Wing of a male from lochan near Oskaig, Island of Raasay, 24.ix. 53. $\times 11$. The outline of the right elytron at the same magnification is shown at 5 A.

FIG. 6.—*Oreclochilus villosus* Müll. Wing of female from Baden, South-west Germany, from R. Richter, 2.vi.52. $\times 11$. The female was of about the same size as the male of *G. natator* but slightly longer and narrower. The outline of the right elytron at same magnification is shown at 6 A.

Hydraena nigrita Germ.

Balfour-Browne suggests that the record for Mull is that of a 'chance immigrant'. I have only dissected a few specimens from Fife, but they had no trace of flight muscles.

Hydraena gracilis Germ.

There are only two records from the Outer Hebrides. I have dissected one specimen from Fife which had frail narrow wings with long cilia on the hind margin (these cilia are also present in other species of the genus) and there were no flight muscles. Balfour-Browne (*in litteris* 28 September 1952), informed me that he had examined three specimens from Dr. Macan and that all were brachypterous. It is hardly likely that this species, which, like *H. nigrita*, lives amongst moss on stones in streams, could be a casual immigrant to the Outer Hebrides and it will probably be found in other localities if carefully looked for.

From the evidence given above it will be seen that there is some reason to doubt whether certain species present in the Western Isles can fly at all. In an investigation of this kind no finality can be obtained and there is always the possibility that a small percentage of specimens capable of flight may exist as in the case of *Noterus clavicornis*. The chances, however, of such inactive species having reached the Western Isles by flight, in sufficient numbers to become established in a suitable habitat, seem to me remote.

Species in which some Individuals are capable of Flight and others are Flightless.

In species which are variable in regard to the condition of the flight muscles, the individuals with normal flight muscles have the muscle supports well developed, most easily seen in the size of the pleural discs. In the beetles in which the muscles are abnormal or absent, the muscle discs are usually, but not always, reduced in size. Both types of reduction may occur in the same species. The possibility of the degeneration of the flight muscles in the individuals with large discs has already been discussed (1952 a). Intermediate forms may also occur in which the flight muscles and their supports are partially developed. In some 'variable' species, the flightless form is the normal one, as in *Noterus clavicornis* (already mentioned p. 77), *Agabus affinis* Payk (p. 89) and *A. paludosus* F. Of the last species I have dissected 21 specimens from Fife, Elgin (R. R.), Berwickshire, Roxburghshire, Hants (F. D. G.), and six from Sweden (C. H. L.). In four out of five of the Hampshire specimens the flight muscles were intermediate. In all the other specimens (with one exception) the flight muscles were abnormal or absent and the discs usually small (fig. 7). The one exception was a specimen taken in a stream near St. Andrews, in December, 1954, which had the flight muscles fully developed. The striking difference in the metatergum and subalar discs of this specimen as compared with the condition found in the usual flightless form is shown in figs. 7 and 8. There are five records of *A. paludosus* from the Western Isles, two of them from Lewis.

In this and in the following section, a species is marked with an asterisk when some individuals have flown in tests; a double asterisk denotes that a species has been taken from an artificial water receptacle indicating natural flight (Grensted, 1939; Macan, 1939; Jackson, 1952 a). J. A. Owen (*in litteris* 27 September 1952) has kindly given me information on beetles collected in a sheep trough near Peebles in the summer of 1951, and when these are new flight records for a species, or of special interest, they have been included.

The following are the 'variable' species:

Haliphus fulvus F.,* *H. confinis* Steph., *H. immaculatus* Gerh.,* *H. ruficollis* Deg.,* *H. wehnckei* Gerh.,** (T. T. Macan, 1939), *Noterus clavicornis* De

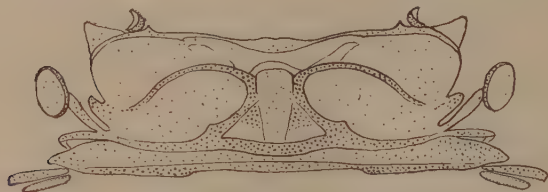


Fig 7

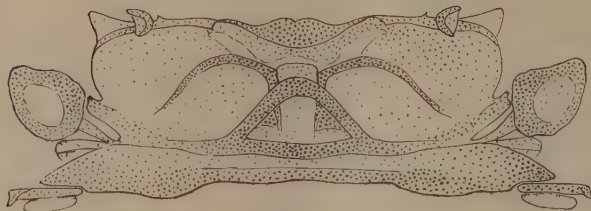


Fig 8

FIG. 7.—*Agabus paludosus* F. Metatergum, internal view, with subalar disc *in situ* but rest of pleuron removed. From a male with no flight muscles from a ditch near Eden estuary, Fife, 18.6.53, $\times 20\frac{1}{2}$.

FIG. 8.—*A. paludosus* F. Metatergum, internal view, with subalar disc *in situ*. From a female with normal flight muscles collected in a stream near St. Andrews on 30.12.54, $\times 20\frac{1}{2}$.

Geer,** (One specimen taken in a swimming bath in Hants by Goodliffe), *Hygrotus inaequalis* F.,* *Deronectes 12-pustulatus* Oliv.,* *Oreodytes septentrionalis* Gyll., *Hydroporus tristis* Payk., *H. umbrosus* Gyll.,* *H. gyllenhalii* Schiod.,* *H. striola* Gyll.,* *H. palustris* L.,** (Owen, 1952; Macan, 1939), *H. erythrocephalus* L.,* *H. longulus* Muls., *H. memnonius* Nic.,** (Grensted, 1939; Owen, 1952, 16 specimens), *H. discretus* Fairm.,* *Agabus affinis* Payk., *A. arcticus* Payk., *A. sturmi* Gyll.,* *A. paludosus* F., *Anacaena limbata* F.,* *Helophorus flavipes* F.,** (Owen, 1952), *Ochthebius dilatatus* Steph.

In most of the above species the flightless individuals predominate so that the chances of such variable species reaching the Western Isles by flight would be reduced, yet some of these species, e.g. *Hydroporus erythrocephalus*, *H. palustris*, *H. gyllenhalii*, *Agabus arcticus* and *Hygrotus inaequalis* are amongst the most frequently occurring species on the islands.

Species in which all the Individuals examined have been capable of Flight.

It is interesting to find that amongst the most frequently occurring species on the islands are such good fliers as *Agabus bipustulatus* L., *Ilybius fuliginosus* F., *Hydroporus pubescens* Gyll., *Gyrinus natator* L. and *G. minutus* F. In addition there are present on the islands twenty-nine species of which all the specimens I have dissected have had normal flight muscles. These are: *Haliphys lineatocollis* Marsh.,** (Macan, 1939), *Deronectes griseostriatus* Deg., *Hydroporus lepidus* Oliv.,* *H. incognitus* Sharp,** (Owen, 1952), *H. nigrita* F.,** *H. planus* F.,** *H. tessellatus* Drap.,** *Agabus biguttatus* Oliv.,* *A. nebulosus* Forst.,** *A. chalconatus* Panz.,** *Ilybius aenescens* Thoms.,** (seen to fly by F. D. Goodliffe), *Rantus exsoleus* Forst.,* *R. bistriatus* Bergstr.,** (S. E. Allen, 1953), *Colymbetes fuscus* L.,** *Dytiscus marginalis* L.,** *D. semisulcatus* Müll.,* at light (L. C.), *Acilius sulcatus* L.,** (Macan, 1939), *Gyrinus caspius*, Mén.,*

G. marinus Gyll.,* *G. opacus* Sahlb.,* (P. B., R. R.), *Hydrobius fuscipes* L.,** (J. A. Owen, 1952, 30 specimens), *Enochrus quadripunctatus* Herbst,* *E. affinis* Thunb.* (*minutus* Brit. auctt.), *Limnebius truncatellus* Thunb.,** (Grensted, 1939), *Helophorus aquaticus* L.,** (Owen, 1952, 57 specimens), *H. minutus* F.,** (taken at light by K. G. Blair), *H. brevipalpis* Bedel,** *Ochthebius minimus* F.* and *Laccobius minutus* L.*

While in almost all the above species flight has been observed, little or nothing is known as to the extent to which many of the species actually fly. Whether all species capable of flight are likely to fly across the sea or to be carried by 'climatic disturbances' remains an open question. At present we know little as to how much species with normal flight muscles actually fly about in their natural habitats,* but the fact that some species with well developed wings and flight muscles remain very local, indicates either that these species do not disperse readily or that they fail to find suitable habitats. From my experience of collecting, principally in Fife, the following species come into this category: *Hydroporus lepidus*, *H. striola*, *Agabus biguttatus* and *Gyrinus marinus*.

A local species may persist in the same spot for years as Balfour-Browne (1953) has observed for *Laccornis oblongus* Steph. Another instance is *Agabus affinis*. This is a 'variable' species of which I have dissected 20, but only found two to have well developed flight muscles. It is usually a rare and local species in Fife. It was taken some 15 years ago in Ross-shire by Mr. D. J. Gordon near Strathpeffer. He showed me the exact spot in June 1952, and I found the species at once. That such a rare and inactive species should have successfully crossed the sea from Ireland or Scotland to become established in Islay seems to me to demand too great a series of favourable chances.

DISCUSSION.

If the water beetles reached the Western Isles by flight it is surprising that quite a number of species which appear to have little or no capacity for flight should be present. Moreover one would expect to find that the islands near the mainland would have a larger number of species than the Outer Hebrides, as the species reaching the Outer Hebrides would be subjected to the greater hazards of the longer crossing, but there is no such inequality in numbers; in fact Lewis and Harris together have 54 species but Skye has only 43, while the small island of Barra, 42 miles west of Ardnamurchan Point, has 46 species. The Outer Hebrides have 71 species, the same number as the Mid Ebrides.

The possibility of the aerial transport of weakly flying species to the Western Isles must now be considered. I have already suggested that weakly flying Halipids may be spread for short distances by wind, and Wellington (1945) who has made a comprehensive study of the conditions governing the distribution of insects in the free atmosphere, considers that short range aerial distribution, as across valleys, is of economic significance. The insects most commonly transported as plankton of the air are Aphididae, Thysanoptera, small Diptera and Hymenoptera. Of the Coleoptera taken, the Staphylinidae were most numerous both in numbers and species (Freeman, 1945). A single specimen of *Helophorus brevipalpis* is recorded by Hardy and Milne (1938) at 250-300 feet over Hull, and the taking of *H. minutus* is referred to by Freeman. Both species are good fliers and neither is common in the Western Isles.

* Flight reduction affecting wings and flight muscles is well-known in certain aquatic Hemiptera and has been extensively studied. Larsén (1950) found that certain individuals of *Ranatra linearis* would not fly though repeatedly tested, yet no noticeable reduction of the flight muscles was found on subsequent dissection. He suggests that, when the skeletal parts of the flying apparatus and the flight muscles appear to be fully developed, and yet the insect shows no inclination to fly, there may be a reduction of the nervous components of the flight apparatus.

Wellington considers that, with rare exceptions, the long range distribution of plankton-zone insects has little chance of success, and he stresses the hazards that must be overcome if the transported insects are to succeed in establishing a colony. Freeman emphasizes the importance of prevailing winds—rather than hurricanes and storms—in the dispersal of insects, and, since in the Western Isles the prevailing winds are westerly, this would not offer favourable conditions for transport from the mainland of Scotland. Unless more evidence comes to light of the aerial transport of water beetles, it seems unlikely that this method of dispersal can have made any important contribution to the water beetles fauna of the Western Isles.

Transport by birds for short distances may be possible in the case of very small species such as *Anacaena* and *Helophorus*, which cling to the water weeds near the surface and might get caught up on the plumage or webbed feet of ducks and other birds, and this may help to spread the species from loch to loch. Transport by logs, or by driftwood, or by human agency, to the Western Isles is most improbable and even if an occasional adult got across it would be almost certain to die without leaving progeny. Balfour-Browne (1950) has shown how difficult it is to establish a colony of water beetles in a new district even when every care is taken to ensure their survival. He took 60 newly emerged specimens of *Agabus undulatus* Schr. from Askham Bog in Yorkshire to ponds in East Norfolk, but subsequent examination of these ponds produced no results. I have myself collected this local species in Askham Bog and all the specimens I have dissected have had reduced wings, modified metathorax and no normal flight muscles, so that it is unlikely that the beetles transported to the Norfolk ponds can have flown elsewhere.

If the water beetles flew across to the Western Isles one would expect to find the best flying species present there, but it is evident that some good flyers, most of which occur commonly on the mainland, are poorly represented, such as *Agabus nebulosus*, *Rantus exsoletus*, *Colymbetes fuscus*, *Hydroporus planus*, *H. incognitus*, *Helophorus brevipalpis* and *H. aquaticus*.

Dr. Guignot (1933, p. 922), though believing the Hydradeephaga to be excellent fliers, notes that a chain of mountains (except for the alpine species) or an arm of the sea appears to oppose an insurmountable obstacle, and he concludes (p. 924) that, excepting for short distances, they can only disperse throughout the world by terrestrial junctions.

The proportion of species with reduced powers of flight occurring in the Western Isles may be taken as evidence that a large part of the water beetle fauna was established there before the land connections were broken. In an earlier paper (1915) Balfour-Browne remarks "If Lewis had recently been part of the mainland which had become separated off by subsidence of an intervening land-tract, the water beetle fauna is just what would be expected". There are however, a few species known from these islands, collected by Dr. G. Heslop Harrison (1936, 1938) which do not occur elsewhere in Britain, *Deronectes canariensis* Bedel, *Hydroporus foveolatus* Heer and *Aulonogyrus striatus* F. These may be relict species of even earlier times. Other species occurring on the islands, such as *Gyrinus urinator* Illig. and *Paracymus scutellaris* Rosenh. (*nigroaeneus* Sahlb.) are unknown from the whole or the greater part of the mainland of Scotland, and Balfour-Browne suggested (1930) that the latter species may be a survival of the preglacial temperate fauna.

Various authorities believe that some members of the British fauna and flora have survived glacial conditions on ice free areas, e.g., Sharp (1901), Bulman (1893), Wilmott (1930), J. W. Heslop Harrison (1948, 1950).

In regard to the probable date of the land connections with the Western Isles, Professor Heslop Harrison, informs me that he considers that the islands were all linked up with the mainland and amongst themselves in the Last Riss-Würm) Interglacial Period, and in at least one of the Interstadial phases

of the last (Würm) Glaciation. Professor J. K. Charlesworth informs me that while nothing is known definitely he considers it possible that a post-glacial land connection existed in Boreal times.

Beirne (1943) concludes that during the Late Glacial Zone II Period [the Second Interstadial Phase of the Last Glaciation (Beirne, 1952)], there were land connections between the Outer and the Inner Hebrides and the mainland of Scotland, and he considers that the greater proportion of the present day Lepidoptera originally entered the British Isles at that time. Flightless land beetles exist on the Western Isles and flightless Carabids have been taken even on St. Kilda (Hudson Beare, 1908), which, together with the presence of other untransportables, such as woodlice and earthworms, and many other examples cited by J. W. Heslop Harrison (1948, 1950), are certainly proof of survival since the time of land connections. Deville (1930) considers that such species as *Hygrotus novemlineatus*, *H. quinquelineatus* Zett., *Deronectes depressus*, *Agabus arcticus* and *Gyrinus opacus* Sahlb. inhabited the ancient northern continent before its dislocation, and that they survived the glacial period on the spot, or almost on the spot, in small privileged zones free from ice and snow during some months of summer. The same opinion is shared by Guignot (1933, p. 965) in regard to boreo-alpine forms, and he points out that at the height of the glaciation, there have always existed on the mountains places free from snow situated above the limits of perpetual snow. In such refuges the beetles have lived in pools and small lakes which would thaw from time to time. Leech (1945) observed that *Agabus vancouverensis* Leech, which occurs on mountains in British Columbia, frequented in June and early July small alpine pools formed by the melting snow, and two were taken in a tiny pool in a rill hardly a yard below its source in the snow. The beetles were feeding, in part, on the bodies of dead insects, Diptera and Hymenoptera, trapped earlier in the snow, refrigerated, and finally washed out. It seems probable that hardy species could have survived arctic periods in the past in the same way. At the present day many of our common Hydradephaga (species occurring on the Western Isles) live at a height of over 2,000 metres in the Alps and the Pyrenees (Bertrand, 1949 a and b), and the same species occur also in the warm waters of the central European plains. This adaptability to great extremes of temperature is noted by Rüschkamp (1926) and will have favoured the survival of species in isolated areas during extremes of climate. Bertrand (1950) observed that lakes in the Pyrenees which remained ice-covered until the summer may contain a rich and varied population of 'Hydrocanthares'. During the glacial period Bulman points out that the summer heat supply would be as great as we receive today, and that a very much larger area of country would be free of ice in the summer than in winter.

Lindroth (1935) considers the boreo-British Coleoptera (including such water beetles as *Agabus arcticus* and *Gyrinus opacus*) are survivors of the Würm glaciation in the British Isles, perhaps on nunataks, and he states that two or three species (including *A. arcticus* (?)) are found as fossils in Sweden outside their present range of distribution, and must have lived there during the last (Riss-Würm) interglacial period. He concludes (1948) that a considerable part of the fauna, including quite temperate species (1939) survived the last glaciation within the limits of Fennoscandia and he mentions (1948) *Agabus guttatus* from interglacial insect remains from Sweden. Balfour-Browne (1934), writing of *Ilybius subaeneus* Er., and *Acilius fasciatus* Deg., states that it is difficult to believe that such hardy species should have failed to survive the Ice Age in this country. Lindroth (1931), in his interesting study of the insects of Iceland, concludes that many species survived the last glacial period there on ice-free coastal strips and he bases his conclusions largely on the present dispersal of certain flightless Carabids and weevils. He states (p. 529) that Dytiscidae are often observed frozen in ice and can endure such

treatment for months. He describes how in Iceland at the present day insect colonies may flourish in the immediate vicinity, indeed within the shelter afforded by glaciers, where moist winds raise the temperature. In his comprehensive work on the Fennoscandian Carabidae (1949) he has interesting views on the advantages possessed by flightless forms during glacial times. He describes the predominance of brachypterous forms of certain Carabids showing wing dimorphism on the west coast of Norway. He considers that the species in question were isolated during the last glaciation (Würm) within ice-free refuges along the Norwegian coasts, and that these small isolated coastal refuges formed islands of organic life where selection was strongly active in favour of flightless insects. During the initial and final phase of every glacial period, on the other hand, the enormous and rapid changes of habitats were in favour of flying insects. He concludes that in repeatedly glaciated areas wing dimorphism must imply a considerable advantage to a species.

It may well be that, in periods of great cold, selection favoured those water beetles in which the flight muscles had failed to develop, as in such individuals the space normally occupied by the flight muscles is largely filled with fat body, and, partly also in mature beetles, by the anterior part of the reproductive organs. Such insects may be more viable and more fertile than those possessing normal flight muscles, and once established in a favourable situation, they would be unlikely to stray and so might withstand severe conditions better than flying individuals. Moreover flight in most species appears to be initiated by warmth and it is improbable that during great cold any specimens which had flight muscles would fly, so that the possession of fully developed flight muscles would confer no advantage; but, once conditions improved, the individuals capable of flight would have a far better chance of dispersing and of colonizing fresh waters as the ice receded. It seems likely therefore that just as in Carabid beetles showing wing dimorphism, the presence of flightless and flying specimens within a species may have enabled some water beetles to survive during periods of changing temperature.

Balfour-Browne concludes that the 'untransportables' (which he believes to be a small minority of the original fauna) must have reached the islands while they still formed part of the mainland of Scotland. If the untransportables have survived in or near the islands one would expect that the hardest of the flying species would also have survived, for they would in all probability, have been more generally dispersed before the onset of glacial conditions and so would have had more chance of continued existence in some favourable spot, probably on land now submerged,* that extended beyond the area of ice.

Balfour-Browne states that there is no way of distinguishing whether species which may yet be discovered on the islands have been overlooked or are new arrivals. There certainly would be no practical means of so distinguishing species in which the wings and flight muscles were fully developed (provided that such species were present on the adjacent mainland and not relict species such as *Deronectes canariensis*); but if additional species are found on the islands in which the flying apparatus is reduced or modified, that would, in my opinion, afford strong evidence for classing them as 'old inhabitants'.

In conclusion, while it is possible that some strongly flying species may have reached the Western Isles by flight, especially the nearer islands, it is doubtful if many of the species present there are good flyers, or can even fly at all. Until more is known regarding the dispersal of the various species, even of those with fully formed wings and flight muscles, there seems to be insufficient grounds for concluding that the great majority of the water beetles have reached the Western Isles by flight, or have been transported there by air currents, in the face of prevailing westerly winds.

* The views of geologists differ in regard to the limit of the westward extension of the Hebridean Ice Sheet and L. R. Wager (1953, *Geol. Mag.* **90**, 177-181) finds no evidence 'hat it reached St. Kilda.

SUMMARY.

Investigations into the condition of the flight muscles in the Hydradephaga and Hydrophilidae have been continued.

Many of the species studied occur in the Western Scottish Islands, and specimens of seventy-five species recorded from these islands have now been examined.

In less than half of these all the specimens investigated have had normal flight muscles, but the remaining species show flightless tendencies; in some species both normal and flightless individuals occur, while in others all the examples so far dissected appear to be incapable of flight.

In such beetles normal flight muscles are absent, and the metatergum and the discs of the pleural flight muscles usually show modifications, and in some species the wings are reduced in size.

It is therefore doubtful if such species can have reached the Western Isles by flight, and it seems more probable that many of them have been established in these islands at the time of land connections, and that they have survived a part at least of the Glacial Period in refuge zones which became free of ice during the summer.

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EXPLANATION OF LETTERING (Figures 1 and 2).

Nomenclature of wing veins according to F. Guignot (1933).

A.	anal vein.	P N P	posterior notal wing process.
A N P.	anterior notal wing process.	Pph.	posterior phragma or postphragma.
A P	apical plate of postnotum.	Psc	prescutum.
C	costa.	R	radius.
Cun	cuneus cell formed by anterior and posterior cubital veins.	R C	radial cell
		R R	recurrent radius
M	media	Sa	subalar disc
O	oblongum cell	Sp	spiracle of 1st abdominal segment.
P. A.	pigmented area at extremity of anterior cubital vein.	Z	spur presenting a section of anterior cubital vein.
P N	postnotum		

Discussion : Professor Frank Balfour-Browne. I congratulate Miss Jackson on her excellent work on the wings and flight-muscles of the water beetles, and it is not until she gets into theory that I differ from her. Her argument is that the power of flight is essential for any water beetle to reach the Western Isles across the intervening seas and she picks out of the water beetle fauna of the Islands a number of species which she has found to be defective in flight muscles. If I take only three example of those she has mentioned I think I can show points which she would have to explain if her whole argument were not founded upon an improbable assumption.

But first for my three examples :—

She referred to our two species of *Noterus*, one of which, the larger, was reported from the island of Raasay in 1935 when several specimens were sent

to me. This was the first Scottish record for the species which had not until then been known north of York. In 1946 it turned up not uncommonly in a small pond in Dumfriesshire, a pond that had only been in existence less than 20 years. In 1949 I found it in numbers in a large pond in Kirkcudbrightshire and in the same year Miss Jackson found it in a loch in Fife. In 1953 it was found in another pond in Kirkcudbrightshire some miles to the west of the previous place and, so far, these are the only Scottish records for that species which has now disappeared from all three southern Scottish localities and, apparently, from Raasay.

Among more than 50 specimens examined by Miss Jackson, only two from southern England have had complete flight muscles.

The smaller species was first found in Scotland in 1942 when I took 2 ♂ and 1 ♀ in a loch in Kirkcudbrightshire. I worked the loch first in 1907 and have visited it many times between that year and the present time. It was worked by Sharp, Lennon, McGowan and some others in those long ago days but none of them reported the *Noterus* which, after its discovery, remained difficult to find until about 1949 when it had become reasonably common on both sides of the loch. In that year Miss Jackson found it in one loch in Fife and as that loch and the one in which she found the larger species are what she describes as old lochs, she assumes that the insects have been there for some thousands of years.

Miss Jackson only had the opportunity of examining four specimens of *Hydroporus ferrugineus* and I have only examined two so that the evidence that this species cannot fly is not very reliable but it is a species that inhabits springs, partly, perhaps mostly, underground and when it is found in a stream or an isolated pool, it is almost always as a single specimen: indicating that such a specimen is out of its normal habitat. In 1881 Sharp found a single specimen on Ben More in Mull and I have twice taken single specimens at elevations above 1,500 feet, once in the Cairngorms, Invernessshire, and once on the Moffat hills, Dumfriesshire. In these three cases the individual was in a pool in a beat bog. How did these specimens reach these pools?

Miss Jackson makes the statement "The proportion of species with reduced powers of flight occurring in the Western Isles may be taken as evidence that a large part of the water beetle fauna was established before the land connections were broken".

It is not disputed that some thousands of years have passed since the Western Isles became islands and Britain became separated from the continent, and Miss Jackson has shown that various stages of degeneration of the flight muscles and of the wings occur in the water beetles and she assumes that all these island species are in the stage of degeneration that they were in before the intervention of the sea. The fact that the insects show all stages of loss of flying powers is evidence favouring the view that the process of degeneration is going on now.

Miss Jackson's reply to Professor Balfour-Browne's remarks:

Professor Balfour-Browne has unfortunately confounded my argument with his own! I set out to question his conclusions that the Western Isles were populated by specimens migrating by flight from the mainland after I had proved that a high proportion of the species recorded from the islands are those in which degeneration of the flying mechanism occurs in specimens collected over a wide range. My argument is that at least some of the species present in the Western Isles have existed there since the period before the land connections were broken.

As regards the larger British *Noterus*, I think it possible, since rare specimens capable of flight occur, that the appearance of this species in the Dumfriesshire pond of recent construction was due to colonization by flying specimens, possibly from some undiscovered colony in nearby marshland.

The assumption that the smaller *Noterus* had been in Lindores Loch in Fife for a long time, undiscovered, is not based on the fact that the loch is of great age but on the fact that all the specimens examined from there are brachypterous. Concerning its occurrence in Kirkcudbrightshire, I would suggest that possibly a species may be present in a body of water for long periods but in very small numbers, just maintaining itself, but that conditions may change to allow it to multiply considerably. In the former conditions collectors might well overlook it, in the latter it would almost certainly be taken in numbers, and it is then easy to assume that the species has extended its range. If, as in this case, the species cannot fly, the assumption that it has extended its range is improbable.

In regard to *Hydroporus ferrugineus* admittedly only a few specimens have been examined but these show pronounced flightless characteristics. This species occurs most commonly in springs. It may either spread by moving in underground water, or perhaps the specimens to which Professor Balfour-Browne refers may have been washed out of the springs by a flood and down to the bog pools which are not their normal habitat.

Professor Balfour-Browne again misunderstands me when he states that I assume that all the island species are in a state of degeneration of the flying apparatus, as I have shown that a number of species occurring on the islands are good fliers. I have produced evidence that the degeneration of the flying apparatus in many other species is very widespread and from this I have concluded that the degeneration is of long-standing. If it occurred before the separation of the Islands, the species must have existed in the area since they reached it by way of the land connection which probably existed in Boreal times. This does not deny that those species of variable flight capacity may still be in process of degeneration of flying powers at the present time. We have no knowledge of the rate of degeneration which may be very slow if its selection value is low.

PLANT DISTRIBUTION IN THE WESTERN ISLES

By W. A. CLARK.

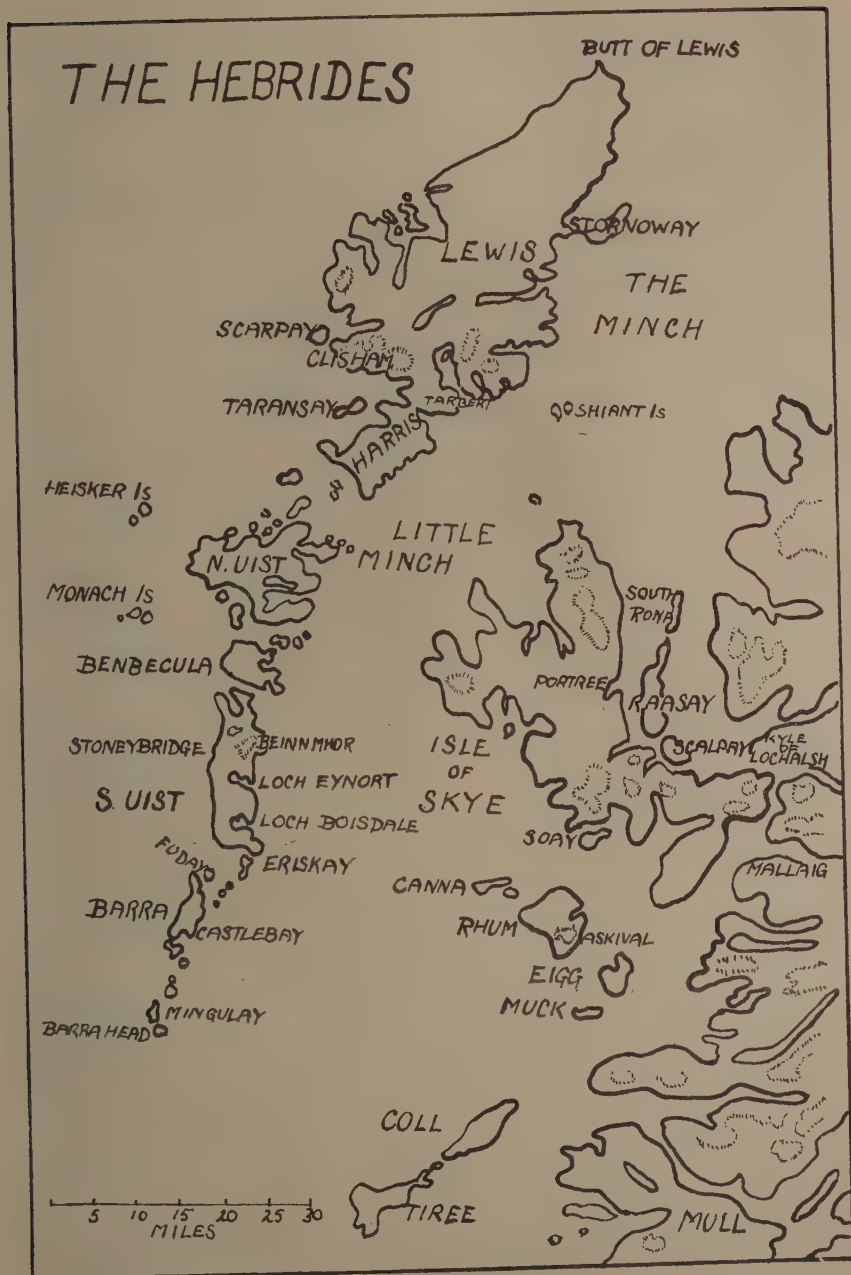
Department of Botany, King's College, Newcastle upon Tyne.

(With 1 text-figure).

Exactly twenty years have elapsed since the work was begun by the biological departments of King's College, Newcastle upon Tyne, under the leadership of Professor J. W. Heslop Harrison, F.R.S., of investigating the flora and fauna of the Western Islands of Scotland. Raasay, lying east of Skye, was the first island to be examined but the work was gradually extended to include all the major islands and many of the smaller ones in the Inner and Outer Hebrides with the exception of the Island of Skye. As the flora of Raasay is essentially similar to that of the neighbouring mainland of Scotland, I do not intend to deal with it now. I should like, rather, to use the time at my disposal to outline some of the more interesting facts which have come to light concerning plant distribution in the Outer and remaining Inner Islands.

The various islands comprising the two groups can be seen on the accompanying map (fig 1). Because of their collective shape, the outer group is often referred to as the Long Island.

Of the various factors determining the plant cover of the islands, climate and geology are the two most important and they will now be briefly considered.



Map of the Hebrides.

The climate is of the extreme oceanic type as the following data, obtained mainly from Manley (1948), clearly show. The annual rainfall of 40–60 in. is lower than one might expect but measurable rain falls on 263 days per year at Stornoway and 243 on Tiree. Another factor which is probably just as important as total precipitation in determining the nature of the vegetation, is the fact that the relative humidity of the air is very high. In Barra the average at 1 p.m. for each of the twelve months lies between 80 and 86 per cent. The oceanic situation of the islands is also reflected in the low annual range of temperature. At Stornoway, with a mean annual temperature of 46.8° F, the maximum winter to summer range is only approximately 15° F. February is the coldest month with a mean temperature of 40.9° F. The data from Castlebay on Barra, and Tiree agree essentially with those from Stornoway except that the monthly means tend to be 1–2° higher. The islands are therefore virtually frost-free and this no doubt is an important factor contributing to the survival there of southern plants like the moss *Myurium hebridarum*. So seldom are the Hebridean plants exposed to frost that an exceptionally severe frost may do considerable damage to the vegetation. Thus, after the severe winter of 1946–47, extensive areas of *Calluna* were killed off on the hills of Harris. It may well be that *Calluna* in the islands is represented by less resistant biotypes as compared to mainland forms.

The factor of wind has been left to the last for this undoubtedly is one of the most important climatic factors affecting the vegetation of these islands. They lie exposed to the full force of the salt-laden, south-west winds. The magnitude of these gales and the height to which the salt spray can be carried can be gauged by the occurrence of *Glaux maritima* on the top of the 700 foot cliffs of Mingulay, in the Barra group. As a consequence of exposure to wind, the islands are virtually treeless and what relict woodland does occur is confined to sheltered gorges and cliffs.

Turning now to the geology of the islands, that of Rhum is the most complex. The rather low-lying north and east of the island consist of Torridonian sandstone and shales. The high hills of the southern half of the island are comprised of complex intrusive igneous rocks of Tertiary origin. In particular, peridotite, eucrite and granite are represented, the first pair, on weathering, breaking down to form fine soils rich in bases. The granite occurs chiefly in the west. In addition, extrusive lava-flows form the summits of Fionchra and Bloodstone Hill. A small area of limestone occurs in the north-west corner and this provides the habitat, as we shall see later, for *Dryas octopetala* and *Saxifraga aizoides*.

Canna consists entirely of volcanic rocks and again these rocks predominate on Eigg and Muck. Coll and Tiree, on the other hand, resemble the Outer Islands in their geological structure, being composed almost entirely of Lewisian gneiss and other rocks of the Archaean complex. We see, therefore, that the Long Island is much less varied in geological structure as compared to Rhum. In general, the higher ground of the Long Island tends to occur in the east. The western shores are characterized by beautiful white shell-sand beaches which give way on the landward side to sandy, peaty pasture called machair. Intervening between the machairs and the higher land to the east is a belt of peaty moorland.

Now we come to the vegetation and from the distributional point of view, botanical interest centres chiefly on three groups of plants, (a) "arctic-alpine" species which occur chiefly on the mountains, (b) a group of plants whose main areas of distribution lie in America—the American species in our flora, and (c) a small group of southern species. Each of these will now be further considered.

The mountains of Rhum provide the principal habitat for the "arctic-alpines" in the Inner Islands. On the Askival-Hallival massif are found the following:—*Silene acaulis*, *Cherleria sedoides*, *Cardaminopsis petraea*, *Oxyria digyna*,

Saxifraga oppositifolia, *S. hypnoides*, *S. stellaris*, *Thalictrum alpinum*, *Alchemilla alpina*, *Saussurea alpina*, *Salix herbacea*, *Deschampsia alpina*, *Juncus trifidus*. In the wetter areas in the Black Corrie below are found *Juncus triglumis* and *Tofieldia pusilla*. This massif consists of ultra-basic peridotite and allivalite which on weathering not only produce the ledges which many of these plants require, but also a soil rich in basic salts—a further factor which undoubtedly contributes to the richness of this mountain flora.

The coll between Ruinsival and Sgurr nan Gillean provides the habitat for *Arenaria norvegica*, only found elsewhere in the British Isles at Inchnadamph, the Shetlands and in the recently discovered station in West Ross. Accompanying it in its Rhum station are *Juncus triglumis* and *J. biglumis*. As the extra-British distribution of this species is confined to Iceland and Norway, it seems probable that this plant may well have survived the last main glaciation in or near its present stations.

The mugearite lava-flows of Fionchra add several more “arctic-alpines” to our list. Here on the drier outcrops are found *Thlaspi calaminare* which strictly speaking should be classed as an “alpine” species, and *Draba incana*, while the north-facing and wetter cliffs support *Poa alpina*, *Poa glauca*, *Saxifraga nivalis*, *S. hypnoides*, *Salix myrsinites*, and *S. arbuscula*.

The list of interesting mountain species is completed by the addition of *Dryas octopetala* and *Saxifraga aizoides*, both of which occur on the limestone in the north-west of the island.

In addition to these flowering plants, the mountains of Rhum provide several very interesting mosses including *Ditrichum zonatum*, *D. vaginans*, *Oncophorus virens*, *Arctoa fulvella*, *Leptodontium recurvifolium*, *L. flexifolium*, *Pohlia drummondii* and *Isopterygium muellerianum*.

The two main centres for “arctic-alpine” species on the Outer Islands lie in the mountains of Harris and S. Uist. On the former are again to be found *Alchemilla alpina*, *Saussurea alpina*, *Saxifraga hypnoides*, *S. oppositifolia*, *Deschampsia alpina*, *Salix herbacea*, *Cardaminopsis petraea* (one station only), *Cochlearia micacea*, *Thalictrum alpinum* and *Luzula spicata* (one station only). The last species has not been recorded from Rhum.

Several of these occur again on the S. Uist mountains with the addition of *Draba incana* and *Silene acaulis* (one plant only observed). The impression gained from a study of the Outer Island “arctic-alpines” is that several are nearing the point of extinction in their present habitats. No doubt this is due, partly at any rate, to the humid climate of these mountain tops but an additional factor on the Ben Mhor massif, would appear to be competition from mosses and liverworts, particularly the latter. On the rock ledges, liverworts often dominate to the exclusion of everything else. Although *Silene acaulis* appears to be dying out on the mountains of the Long Island, it occurs abundantly as a sea-cliff plant on Berneray and Mingulay in the Barra Group and in similar situations in Lewis. *Oxyria digyna* also is found in this type of habitat.

The mountains of the Outer Islands also produce several interesting mosses including *Ditrichum zonatum*, *Arctoa fulvella*, *Dicranum falcatum*, *D. blyttii* and *Bartramidula wilsoni*.

Now we come to the American species, with their two main Hebridean centres on the Islands of Coll and S. Uist. Loch a'Mhill Aird on Coll and some of the lochans in its immediate neighbourhood provide the habitat for *Eriocaulon septangulare*. Accompanying the *Eriocaulon* are *Phragmites communis*, *Deschampsia setacea*, *Juncus articulatus*, *Lobelia dortmanna*, *Nymphaea alba*, *Potamogeton natans*, *P. polygonifolius*, *Littorella uniflora*, *Carex lasiocarpa*, etc. *Hypericum elodes* and *Anagallis tenella* are also present in the wet marginal areas of the loch. Many similar peaty lochs occur on the southern half of Coll but no *Eriocaulon* was detected and, of course, hundreds of lochs

of this type, apparently suitable for *Eriocaulon*, occur on the Long Island. The second member of the American group found on Coll is *Spiranthes stricta* which is also well known as a native of Northern Ireland. It was first detected in the peaty ground along the west shores of Loch Claid but was subsequently found to occur quite abundantly in suitable habitats all up the west coast of the northern part of the Island. A station for this plant has also been discovered in the south of Coll.

Several lochs in the Stoneybridge area of S. Uist, and Loch Searie on N. Uist provide the habitats for *Najas flexilis*, the third Hebridean member of the American element in our flora. These lochs, situated in the transitional region between the sandy machairland and peaty moorland, support a rich aquatic flora, as can be judged by the following list from Loch a'Mhuilinn on S. Uist:—*Potamogeton gramineus*, *P. perfoliatus*, *P. pusillus*, *Isoetes lacustris*, *Callitriche autumnalis* (this plant nearly always accompanies *Najas* in its Hebridean stations), *Menyanthes trifoliata*, *Littorella uniflora*, *Sparganium simplex*, *Chara* spp. etc.

The last of the American species in the Hebrides is *Potamogeton epihydrus* which is new to the British flora although it has been known since the beginning of this century as an adventive in two Yorkshire stations. This pondweed was first discovered in 1944 in a small peaty lochan near Loch Eynort schoolhouse on S. Uist and then subsequently in Loch an Duin, a few miles further to the south. These lochs are again quite typical of hundreds of others which occur in the same vicinity. *Menyanthes trifoliata*, *Carex rostrata* and *Nymphaea alba* are the principal species accompanying *P. epihydrus* in the small lochan.

An outstanding characteristic of all four species is the extremely localized nature of their distribution in the Hebrides, in spite of the fact that suitable habitats are available in abundance on practically all the islands. The restricted distribution of these plants, in spite of the availability of suitable habitats, suggests that they are comparatively recent arrivals in the Hebrides—a view which has also been expressed recently both by Heslop-Harrison (1953) and Iversen of Denmark (1952–53). Both authors are of the opinion that the presence of these plants in the Hebrides and also in Ireland is due to transport of seeds or fruits on the feet of migrant geese, in the Post-Glacial period. The route suggested is from America via Greenland, probably also Iceland, to north-west Britain and Ireland. Iversen puts forward convincing evidence to suggest that many of the aquatic species of S. Greenland, including several pondweeds, must have arrived in that country epizooically on the feet of birds. In particular, he cites the immigration of the annual *Lomatogonium rotatum* into Greenland and Iceland from Canada. This plant prefers wet, clayey soil and it produces a profusion of small seeds. Apparently its migration has so far reached no further than Iceland but Iversen suggests that it should be looked for on the brackish marshes of north-western Scotland.

Transport of seeds in the opposite direction by the returning bird migrants would of course be an equally feasible hypothesis and may very well account for the very restricted American distribution of *Potamogeton polygonifolius* in Newfoundland and the Gaspé Peninsula.

Approximately half a dozen southern species in the sense of Matthews (1937) have been recorded from the Hebridean Islands, e.g. *Desmazeria rigida*, *Agropyron junceiforme*, *Anagallis tenella*, *Phleum arenarium* etc., but with the exception of two moss species, there is nothing to compare with the classical Southern or Lusitanian plants of Ireland. The mosses in question are *Myurium hebridarum* and *Bartramidula wilsoni*. The former is found throughout the Long Island, and on Coll, Tiree, Rhum and Canna in the inner group. It has also been recorded from two stations on the adjacent mainland of Scotland. Outside Britain, it appears to be restricted to the Canary Islands, Madeira and the Azores. This moss, therefore, today possesses a markedly

discontinuous type of distribution. In the Hebrides it occurs in three related types of habitat, viz. on rock exposures near the shore, in similar situations round the margins of lochs and on the rock gullies of the higher mountains. On Ben Mhor in S. Uist, it occurs on the summit cliffs at an altitude of 2000 ft. In this country, this moss has not been known to produce fruit.

Bartramidula wilsoni was found by me on Harris and S. Uist and was also collected independently by Dr. E. V. Watson of Reading on Harris. It is known only from four other localities in the British Isles, and its extra-British pattern of distribution is again discontinuous, with records from Fernando Po, the Cameroons mountains, Yunnan and Hong Kong.

With regard to the history of *Myurium* in the Hebrides, I at one time thought that its occurrence there must be explained in terms of glacial survival. Further study, however, of the distribution of this species in the Hebrides would seem to indicate that it may now be existing there at or near the limits of its climatic range of tolerance. This view is based on the fact that while this plant occurs abundantly in the Outer Islands, it decreases in frequency, in spite of the presence of apparently suitable habitats, as one proceeds in an easterly direction to Rhum and the mainland. Thus, on Rhum it is very rare and on the mainland it has only been recorded from two stations. The principal factor responsible for its decrease in abundance is probably the increase in severity of the winters as one passes to the east and probably due to lesser extent to the decrease in humidity of the air in the east of the area. If this is the case, the chances of per-glacial survival are ruled out and it must be Post-Glacial in origin. Greig-Smith (1950) is of the opinion that many of the Macaronesian liverworts which occur in the British Isles, occupied much more extensive European areas during the warmer and wetter Atlantic division of the Post-Glacial period and that their present discontinuous distribution is due to fragmentation of their earlier more continuous ranges during the cooler and drier climate of the ensuing Sub-Boreal period. It may well be that the distributional patterns of *Myurium hebridarum* and *Bartramidula wilsoni* can be explained in the same way.

So much then for the three groups of plants which are of greatest interest from the point of view of geographical distribution. The rest of the flora, for the most part, is an impoverished version of that of the mainland with oceanic and northern species well represented. The more interesting of the former include *Carum verticillatum* (Loch Eynort, S. Uist only), *Hypericum elodes*, (Coll, Tiree, S. Uist and Barra), *Pinguicula lusitanica*, *Scilla verna*, *Vicia orobus*, *Deschampsia setacea*, *Lobelia dortmanna* (everywhere abundant in the lochs) and *Juncus balticus*. Probably the most interesting of the northern species are *Ajuga pyramidalis*, *Cicuta virosa*, *Drosera intermedia*, *Hammarbya paludosa*, *Vicia sylvatica*, *Carex pauciflora* and the grass *Hierochloë odorata*.

I should like to pass on now to a brief consideration of two species which although common plants on the mainland, are rare in the Hebrides and occur in unusual habitats. The plants to which I refer are *Chamaenerion angustifolium* and *Melandrium rubrum*. Both plants in the Hebrides are confined to cliff ledges. *Chamaenerion angustifolium* has been found in this type of habitat on Rhum, S. Uist, N. Uist, and Taransay. The plant looks markedly different in appearance from the aggressive, mainland, lowland form and may well be a distinct island relict race. I have seen similar plants growing on cliffs high up in the mountains of Clova. *Melandrium rubrum* occurs in similar situations on Rhum and S. Uist and again this plant looks very much different from its mainland relatives.

To conclude, I should like to make brief mention of two rather specialized Hebridean habitats and their respective plant communities. These are the machairland with its pastures and lochs and the sheltered gullies and cliffs with their relict woodland floras.

The machairs occupy, as already stated, the zone lying between the calcareous sandy beaches in the west of the islands (particularly the Outer Islands) and the peaty moorland to the east. The term machair is applied both to fixed dune pasture and to peaty areas which have been covered with a layer of blown sand. As this sand is largely calcareous in nature, the pH of the soil is relatively high and these machair soils support a very rich and varied flora. They also provide the best agricultural land in the islands. In the summer they are virtually ablaze with colour from the buttercups, clover, ladies' fingers, harebells, thyme, gentians and orchids, etc., which flourish abundantly in this habitat. Special mention may be made of such plants as *Juncus balticus*, *Carex maritima* and in the wetter regions various species of orchids, including *Listera orata*, *Coeloglossum viride*, *Orchis strictifolia*, *Orchis purpurella*, and *Orchis fuchsii* ssp. *hebridensis*. These orchids are supplemented on the islands of Fuday and Coll by *Anacamptis pyramidalis*.

The aquatic flora of some of the lochs is also exceptionally rich, particularly of those which occur in the transitional region between the machairland and the adjacent moorland. One of these lochs on Benbecula, Loch na Liana Moire is especially noteworthy for the richness of its pondweed flora. There we found *Potamogeton coloratus*, *P. gramineus*, *P. × billupsii*, *P. natans*, *P. × sparganifolius*, *P. filiformis*, *P. pectinatus* and the hybrid between the last two *P. × suecicus*. In a similar loch on N. Uist, L. Scarie, the rare northern *P. rutilus* was observed in quantity. Elsewhere in Great Britain it occurs only in the Shetland Islands.

Lastly we come to the interesting relict woodland floras of the Hebrides. Evidence from pollen analysis indicates that earlier in the Post-Glacial period, the islands must have been more heavily wooded than at the present time. The occurrence of pine and birch stumps in peat cuttings also bears this out. Today, what trees still remain are confined to sheltered gullies and cliffs. Some very good examples occur on the island of Rhum where the principal tree species are *Betula pubescens* (more rarely *verrucosa*), *Corylus avellana* and *Populus tremula*. *Ilex aquifolium*, *Crataegus monogyna* and *oxyacantha*, and *Quercus petraea* are also often present. Accompanying the trees and sometimes occurring in gullies by themselves, are typical members of the ground vegetation of mainland woods such as *Luzula sylvatica*, *Teucrium scorodonia*, *Endymion non-scriptus*, *Digitalis purpurea*, *Lathyrus tuberosus*, *Vicia sepium*, *Oxalis acetosella*, *Holcus mollis*, *Brachypodium sylvaticum*, *Fragaria vesca*, *Equisetum sylvaticum* and more rarely *Allium ursinum*, *Vicia sylvatica*, *Sanicula europaea*, *Stellaria holostea* and *Vicia orobus*. Ivy, the island form of the common Honeysuckle, and the Royal Fern are also characteristic of such habitats.

The best example of natural woodland in the Outer Islands is found in the Allt Volagir on S. Uist. Again Hazel, Birch and Aspen are present, and the associated ground flora includes *Fragaria vesca* which is very rare in the Outer Islands. Similar habitats again on S. Uist have yielded *Stachys sylvatica*, *Allium ursinum*, and *Agrimonia odorata*.

Three factors would appear to contribute to the survival of these relict woodland floras. These are the all important shelter from the blasting, salt-laden winds, the protection afforded from grazing animals, and lastly, the fact that the peat which blankets the level and gently sloping ground has been unable to develop on the steep sides of the gullies.

May I say in conclusion then, that I have tried in the limited time at my disposal, to give you some idea of the more interesting distributional features which have emerged from our work in the Western Islands.* I hope you will agree with me that the time spent has been very well worth while and that we have been able to demonstrate that these islands hold much of interest to the field biologist.

* Further details can be obtained from the many papers published by the members of King's College, University of Durham, Biological Expeditions in the Proc. Univ. Durham Phil. Soc. 10, 11 and 12.

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ON FIELD STUDIES OF THE DISTRIBUTION OF THE PLANTS AND ANIMALS OF THE SCOTTISH WESTERN ISLES

By J. W. HESLOP HARRISON.

Professor J. W. Heslop Harrison.—For over twenty years I have been engaged in field studies of the distribution of the plants and animals of the Scottish Western Isles with a view to solving two allied problems: (1) the origin and history of the flora and fauna of the islands; and (2) the changes in configuration the area has undergone during the Pleistocene and Holocene periods. A preliminary recital of the results has already been published (Heslop Harrison, 1950) whilst a full account of the distribution of the plants and animals will appear shortly. Concerning these results, it is sufficient to say now that every pertinent fact, botanical and zoological alike, led me to the same conclusion as that put forward by Miss Jackson in the paper just read. This opinion is, of course, diametrically, opposed to that held by Balfour-Browne, i.e. that the populations owe their origin to long-distance random dispersal.

In my judgment, it is quite impossible to maintain that position in face of the massive accumulation of facts drawn from a consideration of numerous groups of plants and animals. At this point we must mentioned the first serious defect in Balfour-Browne's case. He relies on the very restricted testimony of one relatively small group, the Aquatic Coleoptera. Even in that selection, as Miss Jackson has demonstrated, his deductions are unwarranted.

Elsewhere (1953), Balfour-Browne has set out facts, amongst others, extracted from papers of mine, which he imagines support his claims. However, although it is easy to refute the whole of his interpretations, lack of time prevents my doing so now.

It will suffice to deal with one, as typical of the rest. In my paper, I urged that the presence of the Belted Beauty Moth (*Nyssia zonaria*) and the Winter Moth (*Operophtera brumata*) (both species possessing wingless females) in the Outer Isles, the Rhum-Canna group and the Coll-Tiree series of islands was a definite proof of land connections when the species in question were migrating. These land-links I suggested as existing either in the last Interglacial period, or in one of the Interstadial Phases of the Upper Pleistocene Glaciation. Against this, Balfour-Browne propounded the argument that the male Winter Moth may carry the female during copulation and that, doubtless, *Nyssia zonaria* possesses the same means of transport. All that one can say about this is that it demonstrates a complete lack of knowledge of the habits of the Belted Beauty and of its distribution. The insect fails on the Scottish mainland, and on the larger islands, like Skye and Mull, obviously recently separated from it. We are thus expected to believe that the females of *Nyssia zonaria* have been conveyed by the males over many miles of sea from an area in which the species

does not exist, against the prevailing winds and at a colossal speed, for the passage would have to be made during the short period of darkness whilst the insects remain *in cop*. Even the claim raised in the case of the Winter Moth is quite untenable.

The problems presented by the flora and fauna of Iceland are much the same as those of the Hebrides, and the occurrence of the Winter Moth in the birch copses of that island provides a typical example. Clearly, the 'blown over' or 'carried over' explanations must be ruled out. The only acceptable explanation of the outlying Icelandic colonies of *O. brumata* lies in the former existence of land bridges such as we postulated in the case of the Western Isles. At this juncture it is well to point out that the Hebridean distribution of the bee *Bombus smithianus*, which also fails on the mainland, closely approximates that of *N. zonaria*. Although its queens are endowed with wings, the failure of the bee in Skye, Mull, Islay, Jura and Colonsay, strongly supports the evidence afforded by *N. zonaria*.

Turning now to a consideration of other insects, we find that in many orders there exist well-differentiated Hebridean subspecies. Interesting examples of these are seen in the Psyllids, *Anomocera nervosa* and *Livia juncorum*, and the Coccid, *Chionaspis salicis*. Attached as these are to special foodplants, they and these foodplants must have invaded the island areas, more or less simultaneously, over a continuous land mass.

Such a passage, when one takes due cognizance of the drastic effects of earlier over-riding ice sheets, must have taken place during one of the Interstadial (or possibly Interglacial!) phases of climatic amelioration which interrupts the Upper Pleistocene Glaciation.

These Interstadial oscillations, ushered in with high land levels due to the abstraction of the water locked up in the glaciers, must, in their later stages, have been marked by a eustatic rise in sea-levels, depending upon the pouring back into the sea of water from the melting ice load. This would lead to the isolation of many animal and plant species, including those we have just mentioned, and leave them free to evolve independently of any evolutionary movements exhibited by the parent form elsewhere.

These isostatic and eustatic activities, permitting of the appearance of land bridges, seem to have escaped the attention of Balfour-Browne.

Other forms showing geographical subspecies, and supporting the evidence just adduced, are to be noted in the butterflies, *Maniola jurtina*, *Coenonympha pamphilus*, *Argynnis aglaia*, *Polyommatus icarus*; the moths *Eupithecia pulchellata*, *Epirrhone alternata*, *Perizoma albulata*, the bee *Bombus jonellus*, the dragon fly, *Sympetrum striolatum* ssp. *nigrofemur*, the wood mouse *Apodemus sylvaticus* and many others.

Again, if random dispersal is invoked to account for the island floras and faunas, how are we to explain the occurrence of many plants with their proper parasites? Amongst these are gall-wasps like *Rhodites rosae* on *Rosa sherardi*, the sawfly *Euura atra* on *Salix repens*, the gall-fly *Dasyneura populeti* on aspen, the gall-mite *Eriophyes thomasi* on *Thymus serpyllum* and numerous specialized rusts, exemplified by *Puccinia epilobii* on various willow herbs.

It is inconceivable that these parasites and hostplants travelled separately by chance, managed to survive, and then finally met again by chance.

The only reasonable explanation is that they migrated, *pari passu*, over a continuous land bridge to occupy their present stations.

The Viviparous Lizard occurs on Rhum, Coll, Vatersay and other islands, as does the Slow-worm on Lewis and Harris. Is it thinkable that these reached their island abodes otherwise than over definite land routes? The same applies to newts on Rhum, Canna, Eigg, etc.; on these islands both the Smooth Newt and the Palmate Newt are not uncommon. Most certainly they

colonized these islands *via* an overland passage. Of the same import* is the evidence of the worm populations. Earthworms are plentiful both in the Inner and Outer Hebrides, and numerous species have been recorded. They, of all animals, demand an uninterrupted land route.

Now let us take up the evidence supplied by Hebridean plants. In this connection, the most important is the moss *Myurium hebridarum*, with a Hebridean range essentially the same as that of *Nyssia zonaria* and *Bombus smithianus*. Elsewhere, it has only been recorded from the Macaronesian islands, the Azores, Canary Islands and Madeira. This not only points to an early Tertiary origin, but suggests land bridges of a very far-reaching kind. Further, as the moss reproduces solely by vegetative means it can only extend its range by similar means. This, in turn, implies that, no matter in what stations the moss survived the Ice Age, it reached its present Hebridean stations when the islands were linked together in a continuous whole.

In the case of other plants, it may be argued that chance dispersal by wind would account for their existing habitats. Possibly this may be true in some instances, but certainly not in others. Firstly, attention is directed to the viviparous grasses *Poa alpina* and *Festuca vivipara*. Their ranges can only depend upon former land connections.

The same applies to all the Alpine rarities, like *Saxifraga hypnoides* and *S. aizoides* found in the Outer Isles, and to the many plants of similar proclivities recorded from Rhum, Eigg and other islands in the Inner series.

Further, the Dactylorhichs yield pertinent evidence. Of special importance is the Hebridean Spotted Orchid *Dactylorhichs fuchsii* ssp. *hebridensis*. Its distribution is very instructive; except that the plant is lacking in the Rhum-Canna group, its Hebridean range coincides with that of the moth *Nyssia zonaria*. However, it just touches Donegal in Ireland, and Sutherland on the Scottish mainland. Obviously, it can only have developed such a distributional pattern during the Upper Pleistocene Glaciation. This indicates in turn that, not only did inter-island connections exist then, but also that these links extended to Ireland and Scotland.

Curiously enough, in the Rhum group no form of the diploid *D. fuchsii* occurs; that species is replaced by the endemic subspecies *rhounensis* of the allied tetraploid species, *D. ericetorum*. This circumstance demonstrates that the Rhum isles once underwent an earlier stage of isolation, when they were separated, as today, from both the other islands and the mainland, during which the evolution of this subspecies took place.

Another informative species is the Vernal Squill, *Scilla verna*. It exhibits a fringing distribution in all the significant Outer Isles and in Coll, Tiree and Canna, passing thence *via* Sutherland, Caithness, Orkney and Shetland to the Faroes and Norway. As it possesses a heavy seed it can only have progressed to these widely separated, but orderly arranged stations, overland. Moreover, its absence from the West of Ireland and its curious distribution in the Irish Sea area demand a former land bridge between Scotland and Ireland.

As a final line of proof of the existence of former land bridges, let us consider the result of peat investigations based on pollen-analytic methods. These reveal a systematic immigration of forest trees into the Inner and Outer Isles in post-glacial times. More especially to be emphasized is the fact that, starting from zero in the early Boreal Period, oak pollen reaches the high level of 20 per cent in Barra and South Uist during the Atlantic Period (Zone VII of Godwin). Considering the mode of dispersal of acorns, and their short period of viability, it seems incredible that oak should have invaded the Outer Isles, Coll, Rhum, etc. other than over dry land in favourable Boreal times. Although

* Since this was written a further extremely important discovery has been made; the mussel (*Anodonta cygnaea* L. has been detected in the Grosebay Burn and elsewhere in South Harris. This observation lends powerful support to the views put forward above.

oaks no longer occur native in the Outer Isles, the ordinary ground flora of an oakwood comprising hazel, honeysuckle, bluebell, garlic, primroses and the like still persists in diverse stations like the Allt Volagir ravine on South Uist.

Further, in many islands, as for instance Lewis, Harris and Rhum, the holly (*Ilex aquifolia*) is not infrequent, whilst the ivy (*Hedera helix*) is even more abundant. As Faegri (1940, 1943) and Iverson (1944) have shown, these species were moving northward in the Western European area in Boreal and Atlantic times. Once more only a continuous stretch of Hebridean land, of post-glacial development, is capable of explaining their present distribution in the Hebrides.

In conclusion, it is clear, from the many lines of evidence invoked, that links between the Hebrides and the mainland must have existed in various positions not only during the Glacial Period, but also in early post-glacial times.

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